Historic, archived document

Do not assume content reflects current scientific knowledge, policies, or practices.

GENETICS

of LODGEPOLE PINE

A99.9 F76Us

PSW FOREST AND RANGE
EXPERIMENT STATION
MAR 5 [illegible]81
STATION LIBRARY COPY

R-5

U.S. Department of Agriculture
Forest Service

Research Paper
WO-37

This publication is one in a series on the genetics of important forest trees of North America being published by the Forest Service, U.S. Department of Agriculture, in cooperation with the Society of American Foresters. Development of this series is in accord with the resolutions of the World Consultation on Forest Genetics and Tree Improvement at Stockholm in 1963 and the Second World Consultation on Forest Tree Breeding at Washington, D.C., in 1969. The Committee on Forest Tree Improvement of the Society of American Foresters undertook the preparation of manuscripts for North American species.

Contents

Page

RESEARCH SUMMARY iii
INTRODUCTION 1
  Natural distribution and habitat 1
  Taxonomy and evolution 3
  Fossil history 4
SEXUAL REPRODUCTION 6
  Reproductive development 6
  Cone and seed production 9
  Self- and cross-pollination 15
  Controlled pollination 15
  Germination and establishment 16
VEGETATIVE PROPAGATION 18
  Grafting 18
  Rooting 18
  Tissue culture 19
VARIATION IN NATURAL STANDS 20
  Growth, form, and longevity 20
  Wood and bark 21
  Leaves 22
  Reproductive structures 23
  Resin 25
  Pests 25
  Natural hybridization and introgression 27
VARIATION IN PROVENANCE TESTS 29
  Survival and hardiness 29
  Growth, yield, and form 31
  Needles 35
  Wood, bark, and resin 37
  Reproductive characters 37
  Pests and air pollution 38
  Local variation 39
  Land-races 39
CONTROLLED HYBRIDIZATION 41
CYTOGENETICS 43
GENETIC IMPROVEMENT 44
ACKNOWLEDGMENTS 47
LITERATURE CITED 47

For sale by the Superintendent of Documents, U.S. Government Printing Office
Washington, D.C. 20402

November 1980

Resea

The mo
America.
noteworth
the coast
margina
evolved i
tions. The
Rocky Mo
gnal com
y forest
n most s
rolled by
Cascades
pen at m
Lodgep
has it bee
northwes
same see
n cold c
years, a
he Britis
The o
million ye
species w
it was a
nating.
range by
from far
Lodge
with on
Virginia
moderat
naturally
tain sta
but the
uncertai
but polle
Sierra N
most oth
Chrom
nuclear

Research Summary

The most widespread conifer in western North America, lodgepole pine (*Pinus contorta* Dougl.) is noteworthy for its broad ecological amplitude. In the coastal region, it is largely confined to marginal sites, and localized ecotypes may have evolved in a variety of edaphically extreme situations. The wide distribution of the species in the Rocky Mountain-Intermountain region—its principal commerical range—is attributed primarily to forest fires, and serotinous cones are present in most stands. Distribution appears to be controlled by factors other than fire in the southern Cascades and Sierra Nevada, where the cones open at maturity.

Lodgepole pine is a small tree, and only recently has it been heavily utilized in its native range. In northwestern Europe, however, the ability of some seed sources to grow well on poor sites and in cold climates has interested foresters for many years, and the species is now widely planted in the British Isles and Sweden.

The oldest fossils of lodgepole pine are several million years old, but there is no evidence that the species was widespread until the late Pleistocene. It was an important pioneer following glacial melting, and occupied its extensive northern range by migration from the south and possibly from far-northern refugia.

Lodgepole pine has been successfully crossed with only two other species: jack pine and Virginia pine. Crossability with jack pine is moderately high, and the two species hybridize naturally in Canada. Many northern Rocky Mountain stands have jack pine-like characteristics, but the extent of introgression from jack pine is uncertain. Lodgepole × jack hybrids are fertile, but pollen abortion is sometimes high. Hybrids of Sierra Nevada parentage have not grown well in most other environments.

Chromosome number, amount of DNA, and nuclear size are constant in the species. Most races are sexually precocious, and some produce pollen in enormous quantities. Seed is produced regularly in large amounts, and losses to cone and seed predators are usually small. Germination requires light, but not stratification, and has a narrow range of optimum temperatures. Much of the seed stored in serotinous cones (up to several million per ha) retains its viability for many years. The winged seed is small, highly dispersible, and known to travel distances of 16 to 18 kilometers.

Three well-differentiated, interfertile geographic races have evolved in the coastal, Rocky Mountain-Intermountain, and southern Cascade-Sierra Nevada regions. They differ in tree longevity, dimensions, form, and branchiness; needle size and structure; cone form, density, orientation, persistence, and serotiny; the timing of reproductive events; seed size and germination behavior; resin composition; and parasites and predators.

Many characteristics of lodgepole pine make it suitable for use in genetically improved, short-rotation plantations. Selection is relatively easy in even-aged natural stands, juvenile growth of most races is rapid, adequate seed production begins early, vegetative propagation is not difficult, and selfing ability is low. Much of what is known about genetic diversity in the species has been learned from European provenance tests, some of them several decades old. These tests have shown that (1) much of the variation in natural stands has a genetic basis, and (2) characteristics such as mortality and growth rate exhibit large genotype × environment interactions when they are compared across northern Europe. The possibilities of interprovenance hybridization are being explored in Britain, and a Swedish improvement program is selecting trees in native North American stands for use in Sweden.

The Genetics of Lodgepole Pine

William B. Critchfield[1]

Introduction

Lodgepole pine (*Pinus contorta* Dougl.) is the most wide-ranging and one of the most variable of the American pines, with an elevational distribution—from sea level to timberline—that brackets the entire range of tree growth in western North America. It is a major forest resource throughout much of the interior West: forests dominated by this species cover about 15 million acres (6 million ha) in the United States and nearly 50 million acres (20 million ha) in Canada. Lodgepole pine is a small tree compared with most of its associates, and until the past two decades its wood was utilized less than that of any other western timber species. Increased interest in the species as a timber tree is reflected in a recent symposium summarizing current knowledge of the growth, ecology, and management of lodgepole pine in its native habitats (Baumgartner 1975).

The genetic makeup and improvement of lodgepole pine have not received much attention in North America until the past decade. Outside its native range, the ability of some strains to grow well on poor sites and in cold climates has interested foresters in northern Europe for more than 50 years, and lodgepole pine is now widely planted in parts of Britain, Ireland, and Scandinavia. Much of the available information about the genetic diversity of the species comes from provenance investigations in northern Europe and elsewhere. The early results of this research were summarized by Edwards (1954, 1955).

This paper emphasizes what has been learned in the past two decades about the reproductive biology and genetics of lodgepole pine. Unpublished sources have been heavily utilized, including data of the Institute of Forest Genetics (IFG) at Placerville, Calif.

Natural Distribution and Habitat

Lodgepole pine is notable for its unusually wide ecological amplitude, both climatic and edaphic. The latitudinal range of the species, from about 31° N in Baja California to about 64° N in the Yukon (fig. 1), is exceeded among other pines only by *P. sylvestris*. No other pine matches it in elevational range. At many places along the Pacific coast, it approaches sea level, and in the southern Sierra Nevada it reaches its upper limit at 12,000 feet (3,900 m) (Howell 1946).

Within these broad limits, lodgepole pine grows in three principal regions: (1) the Pacific coast from Yakutat Bay, Alaska, to northern California, including the entire region west of the Coast Mountains of Alaska and British Columbia, the northern Cascade Range, and the Coast Ranges of southern Oregon and northern California; (2) the mountain chain comprising the Cascade Range, Sierra Nevada, and the high mountains of southern California and northern Baja California; and (3) the Intermountain region and Rocky Mountain system from the central Yukon to eastern Oregon and southern Colorado, with eastern outliers from the Caribou Mountains of northern Alberta to the Black Hills of South Dakota.

In the coastal region, where the species is sometimes called shore pine, it occupies a variety of extreme habitats that are all unfavorable for the growth of possible competitors. In the far north, bogs and muskegs are its principal habitat (Wood 1955). Farther south it grows on cliffs, sand dunes, and rocky sites. Inland from the immediate coast, it extends up to elevations of 5,000 feet (1,500 m) on southern Vancouver Island (Garman 1973). It grows on serpentine soils in the San Juan Islands, and on excessively drained, nutrient-poor glacial drift in the Puget Sound region (Franklin and Dyrness 1973). In the low coastal mountains

---

[1] Geneticist, Pacific Southwest Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service, Berkeley, Calif.

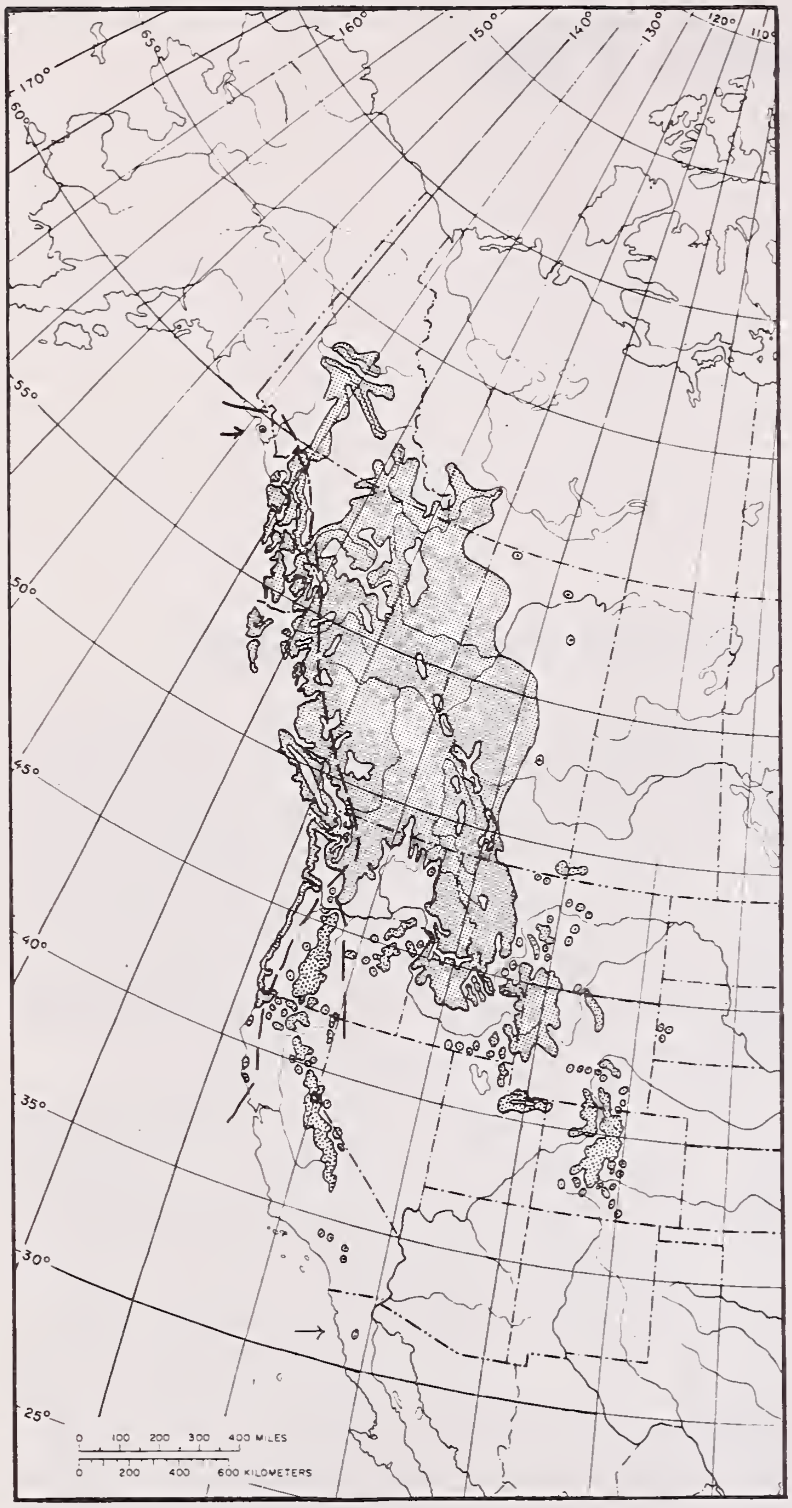

Figure 1.—Distribution of lodgepole pine (from Little 1971). Broken lines mark approximate boundaries of coastal, Sierra-Cascade, and Rocky Mountain-Intermountain races. More recent range extensions have been reported in northern and northeastern Alberta (Achuff and La Roi 1977, North 1976), southwestern MacKenzie District (Scotter 1974), the central and western Yukon and northwestern British Columbia (von Rudloff and Nyland 1979; E. Nyland, pers. commun., Sept. and Nov. 1976, Nov. 1977). In the Yukon, lodgepole pine is now known to extend as far north as 64° 10′N on the Dempster Highway east of Dawson, and west to 138° 50′ W in the region north of Kluane Lake.

of northwestern California, it occurs on serpentine and other ultramafic soils; and near its southern coastal limits, a dwarf form grows on the Mendocino White Plains a few kilometers inland from the coast. This unique pygmy forest has "one of the most acid soils known anywhere," an extremely infertile podzol with a cemented hardpan, and a pH of 2.8 to 3.9 (Jenny and others 1969).

Outside the coastal region, lodgepole pine is more generally distributed. In the Cascade Mountains of Washington and Oregon, it is an important seral species in several forest zones on the drier eastern slopes. Its status is more permanent on marginal sites, including serpentine soils in the Wenatchee Mountains (Franklin and Dyrness 1973), and both droughty, sandy soils and poorly drained, highly organic soils in the northwest Oregon Cascades (Stephens 1966). East of the Cascades in south-central Oregon, lodgepole pine forms extensive edaphic or topographic/edaphic climax forests on the pumice deposited by Mt. Mazama 6,600 years ago (Franklin and Dyrness 1973). Some of these soils are poorly drained or seasonally wet, but on other sites the dominance of lodgepole pine may be related to the low-temperature tolerance of its seedlings compared with those of ponderosa pine, its principal competitor in this region (Berntsen 1967, Cochran and Berntsen 1973).

Lodgepole pine is also common at upper elevations in the California mountains, but its ecological status in this region has received little study and is poorly understood (Rundel and others 1977). Throughout a broad elevation range, it is the most common tree on sites with shallow water tables, such as meadows, lakeshores, and stream benches. It also dominates the poorly defined lodgepole zone, above the red fir zone and below the subalpine forest. In the lodgepole zone, it often forms extensive pure stands in glacially scoured basins, as in the Yosemite region. The species is a minor component of the Sierra Nevada subalpine forest, occasionally extending to timberline; and in the high ranges of southern California, it is the primary constituent of subalpine forest (Thorne 1977).

Most of the commercial range of lodgepole pine is in the Rocky Mountain-Intermountain region, where its wide distribution is attributed primarily to forest fires. Serotinous cones, present in many stands, provide a seed reserve released by fire.

Other attributes that make the species an aggressive pioneer in this region are the regular and abundant production of seed from an early age, the small size and high dispersal ability of the seed, and relatively rapid juvenile growth.

Throughout the region, from the Yukon (Porsild 1951) to the Blue Mountains of eastern Oregon (Trappe and Harris 1958) and Colorado (Clements 1910), lodgepole pine is considered an intolerant, successional species. Virtually all of the extensive lodgepole forests in Alberta are believed to be seral and of fire origin, with the species persisting longest on the wettest sites (such as bog margins) and driest sites available (Horton 1956, Smithers 1961). Lodgepole pine is considered a climax species in a few of the plant communities that it dominates, and Moir (1969) suggested that it forms a narrow zone of climax forest at elevations of 8,200 to 9,300 feet (2,500 to 2,800 m) in the Front Range of Colorado, with a successional role in forests above and below this zone. But most of the extensive—and apparently permanent—stands of lodgepole pine in the region are interpreted as prolonged seral stages (Hoffman and Alexander 1976, Pfister and Daubenmire 1975, Pfister and others 1977). An alternative interpretation is that lodgepole pine is able to maintain dominance indefinitely on many sites because it has evolved a set of characteristics that make it (1) periodically fire-prone and (2) able to perpetuate itself after fire (Brown 1975).

The adaptability of lodgepole pine to a wide variety of sites can be attributed partly to characteristics of its leaves and root system. Seedlings from eastern Oregon had a moderate to high transpiration rate, but water loss was closely controlled (Lopushinsky 1975). The stomata closed at a relatively high level of water availability, and at night they closed completely. Sierra Nevada lodgepole pine also exhibits remarkable control of its internal water balance over a wide range of soil moisture conditions (Rundel and others 1977). Oregon-coast seedlings were much less sensitive to depth of water table (Minore 1970) or prolonged flooding (Minore 1968) than seedlings of associated conifers, and the shoot growth of Washington-coast seedlings was much less reduced by prolonged flooding than that of *P. sylvestris* seedlings (Vester and Crawford 1978). The roots of lodgepole seedlings grew better than Sitka spruce at low oxygen concentrations (Macaulay Institute 1969), and could be gradually induced to grow into soil devoid of oxygen (Forestry Commission 1975). Under these conditions, cavities developed in the stele of the adapted roots, and oxygen may have been transported internally from aerated parts of the plant.

Taxonomy and Evolution

P. contorta has been subdivided into as many as four species in the past (Critchfield 1957), reflecting the conspicuous, geographically ordered variation in what is now usually accepted as a single species. This variable entity has been classified in three ways:

(1) A single species with no infraspecific categories (e.g., Little 1953).

(2) Coastal and inland forms recognized as separate varieties (*contorta* and *latifolia* or *murrayana*) or species (*P. contorta*, *P. murrayana*) (e.g., Munz 1959).

(3) Coastal, Mendocino White Plains, Sierra-Cascade, and Rocky Mountain-Intermountain forms recognized as separate taxa of varying rank (species, subspecies, or varieties).

In a classification based mostly on leaf and cone characteristics of natural populations, Critchfield (1957) followed the last approach:

P. contorta ssp. *contorta:* Pacific Coast
P. contorta ssp. *bolanderi:* Mendocino White Plains
P. contorta ssp. *murrayana:* Southern Cascades, Sierra Nevada, mountains of southern and Baja California
P. contorta ssp. *latifolia:* Rocky Mountain and Intermountain regions, northern Cascades

These taxa are referred to in this paper as the coastal, Mendocino White Plains, Sierra-Cascade, and Rocky Mountain-Intermountain races. A distinctive population growing on ultramafic soils in the low coastal mountains of Del Norte County, in the northwestern corner of California, may also warrant taxonomic recognition (Critchfield 1957). It is referred to here as the Del Norte race.

The only close relative of lodgepole pine is jack pine (*P. banksiana*), which ranges from the Atlantic coast nearly to the Arctic Circle in the Mackenzie District of Canada. Lodgepole and jack pines are morphologically similar, hybridize where they overlap in western Canada, can be artificially crossed with ease, and produce fertile F_1 and later-generation hybrids. Despite these indications of a close relationship, their status as distinct species has seldom been challenged. An exception is Boivin's (1966) lumping of the two as a single species, a classification that has not been widely accepted.

P. contorta and *P. banksiana*, together with *P. virginiana* and *P. clausa* of southeastern North America, were placed by Duffield (1952) in his group XIII, later named subsection Contortae by Little and Critchfield (1969). The species comprising Contortae have all been linked directly or indirectly by hybridization. Like the two northern species, *P. virginiana* and *P. clausa* cross readily (Critchfield 1963). The first verified hybrids between the northern and southern species in Contortae were produced at Placerville only recently (unpublished data, IFG). Crosses between *P. contorta* and *P. virginiana* produced chlorotic, dwarfish offspring, perhaps indicating a remote relationship between the parent species.

P. contorta and *P. banksiana* have a Eurasian analog in *P. sylvestris* of subsection Sylvestres. The most widely distributed and northerly of pines, *P. sylvestris* shares several features with the northern Contortae: short needles in pairs, small cones and seeds, and distributions that are mostly or entirely in regions that were periodically covered by ice during the Pleistocene. These similarities led Clausen (1963) to group these three pines in a cenospecies "representing a single large gene pool." He later (1968) expanded the group to include other Eurasian members of Sylvestres.

The facts of pine morphology, cytology, and crossability do not support Clausen's grouping, and the fossil record provides no convincing links between the northern Contortae and the Eurasian species of Sylvestres. The latter group, despite its large size, is morphologically coherent, its karyotype is unique in the genus, and none of its members has been hybridized with any other pine (Wright and Gabriel 1958). The Sylvestres pines all have two pairs of heterobrachial chromosomes, whereas all other pines studied have only a single pair (Saylor 1964).

A few authentic hybrids have been produced between *P. clausa* of subsection Contortae and *P. elliottii* of subsection Australes (Saylor and Koenig 1967), a large group that includes most of the pines of southeastern North America. This slender link suggests that Australes, among extant pine lineages, is most closely related to Contortae.

Fossil History

Macrofossils of *P. contorta* are remarkably few, although the species often grows in habitats (bogs, lakeshores) that are over-represented in the fossil record. The best known Tertiary macrofossil attributed to this lineage is a cone of *P. premurrayana* from the Yellowstone region (Knowlton 1899). It cannot be dated with any confidence (H. D. MacGinitie, pers. commun., June 1973), and does not closely resemble the cone of *P. contorta* or any other extant pine. Seeds and a cone fragment in the upper Eocene Bull Run flora of northern Nevada may possibly represent a lineage ancestral to *P. contorta* (D. I. Axelrod, pers. commun., Feb. 1972).

The species makes its first unequivocal appearance in the fossil record as a constituent of the conifer-rich forests that extended from the Pacific Northwest to Alaska in the late Tertiary. It is represented by a single cone in the late Miocene Faraday flora near Portland, Oregon (J. A. Wolfe, pers. commun., Nov. 1971). Pollen closely resembling that of native *P. contorta* is abundant in the late Miocene/early Pliocene Skonun flora of the Queen Charlotte Islands (Martin and Rouse 1966). Pollen of the *Diploxylon* (= subgenus *Pinus*) type is also represented in the Pliocene Lava Camp Mine flora on the Seward Peninsula of western Alaska (Hopkins and others 1971). If the tentative identification of this pollen as *P. contorta* is correct, this is the only fossil occurrence of the species far outside its present range. The nearest stands today are in west-central Yukon, nearly 700 miles (1,300 km) to the east. Another Pliocene flora, Alvord Creek in eastern Oregon, includes a seed *(P. alvordensis)* that somewhat resembles a seed of *P. contorta* (Axelrod 1944).

During the Pleistocene, abundant cones of unknown age were deposited along the Oregon coast (J. A. Wolfe, pers. commun., Oct. 1971), and pollen identified as *P. murrayana* is plentiful in several early Pleistocene floras in and near the southern Sierra Nevada (Axelrod and Ting 1961).

In the last interglacial interval of the Pleistocene, *P. contorta* may have extended 60 to 250 miles (100 to 400 km) beyond its present northern limits. Considerable pine pollen is present in pre-Wisconsin deposits in eastern Alaska (Matthews 1970) and the northern Yukon (Lichti-Federovich 1974), and *P. contorta* is the only pine in this region today.

Not until late Pleistocene and postglacial times is there much evidence that *P. contorta* was widespread and abundant. In these recent deposits it is chiefly represented by pollen. Identification of pine species by pollen characteristics is often questionable (Mack 1971); but where *P. contorta* is the only pine present, its identity can be inferred with more certainty.

By the end of the Pleistocene, *P. contorta* is thought to have been widespread south of the ice in western North America, and this must have been one of the principal bases from which it reoccupied its northern range. The older pollen studies of Hansen (bibliography in Hansen 1967) and more recent work of Heusser (1965, 1973) and Mathewes (1973) established that a pine identified as *P. contorta* commonly initiated forest succession on glaciated terrain throughout the Pacific Northwest, and was gradually replaced in early postglacial time by the conifers that still dominate the forests of the region. This view of postglacial succession in the Pacifc Northwest was challenged by Mack and others (1976), who found no indication that *P. contorta* was a significant element of early postglacial vegetation at an eastern Washington site earlier studied by Hansen. However, the presence of *P. contorta* needles in early postglacial lake sediments confirms that this species pioneered forest succession in the Fraser River lowland within a few hundred years after the retreat of the ice (Mathewes 1973), and it probably played a similar role at other sites west of the Cascades.

P. contorta was also an early dominant in postglacial forest succession in the Rocky Mountain region. It is abundantly represented by pollen in deposits in southeastern Idaho (Bright 1966), the Yellowstone region (Baker 1970, Waddington and Wright 1974), and northern Idaho and Montana (Heusser 1969), and its identity is confirmed by fossil needles in the Yellowstone region (Baker 1976).

Other refugia from which *P. contorta* may have recolonized its northern range at the end of the Pleistocene include: (1) unglaciated parts of the Yukon, (2) ice-free areas east of the Canadian Rocky Mountains, between the Cordilleran and Laurentide ice sheets, and (3) the north Pacific coast. If the species survived the last glaciation in one or more northern refugia, the genetic structure of present-day northern populations may still reflect the intermingling of several isolated and possibly differentiated strains.

The evidence for northern refugia is inconclusive. Contemporary populations in and near unglaciated portions of the Yukon are distinctively different in needle-resin composition and a high incidence of three-needled fascicles (von Rudloff and Nyland 1979), but there is no pollen evidence supporting Hultén's (1937) suggestion of a Yukon refugium. Only trace amounts of pine pollen are present in late-glacial and postglacial sediments at sites about 60 miles (100 km) north and west of the species limits (Terasmae 1973, Rampton 1971), and pine did not reach the Atlin region, just south of the Yukon border, until 4,200 to 2,000 years ago (Anderson 1970). The existence of an ice-free corridor east of the Rocky Mountains is debated by geologists (Hopkins 1967, Reeves 1973, Stelck 1967), and the pollen record indicates that pine *(P. contorta* or *P. banksiana)* did not reach east-central Alberta until 7,500 years ago (Ritchie 1976). Pines were early invaders of deglaciated ground on the northern Pacific coast, and grew near Juneau, Alaska, more than 10,000 years ago (Heusser 1965), but the origin of these populations is unknown. Geological evidence provides little support for the existence of unglaciated enclaves in this region during the late Pleistocene.

Sexual Reproduction

Reproductive Development

Lodgepole pine is more sexually precocious than most other pines. Righter (1939) reported a minimum age of 4 years for male and female strobilus production on trees growing at Placerville, California. Extreme precocity was recently observed in the same environment. Lodgepole seedlings produced male strobili and functional pollen at less than 1 year, and lodgepole × jack pine hybrid derivatives of the same age produced female strobili with functional ovules (Johnson and Critchfield 1979).

Open-grown lodgepole pines in Colorado occasionally produce cones at 5 years, but usually even open-grown trees do not begin to produce cones until they are about 15 years old (Clements 1910). Cone-bearing may begin earlier farther north: open-grown trees in the northern Rocky Mountains commonly produce cones at 5 years (J. E. Lotan, pers. commun., Aug. 1978). In Alberta, cone production was general in a moderately dense subalpine stand (7,000 stems per acre) when the trees were about 12 years old and 7 feet (2 m) tall, but even much smaller and younger trees bore occasional cones (Crossley 1956a). In Britain, some coastal provenances (Lulu Island near Vancouver, British Columbia, and southeastern Vancouver Island) produce abundant male and female strobili at 5 or 6 years (R. Lines, pers. commun., June 1978). In a plantation at Placerville made up of the geographic origins described by Critchfield (1957), 80 percent of all coastal trees were flowering by the age of 6, and many had begun 1 or 2 years earlier.

Unlike many pines, lodgepole pine does not regularly first produce female strobili when it reaches reproductive age. In the same plantation at Placerville, 6-year-old trees producing both kinds of strobili were about equal in number to trees with only female strobili, and a few produced only males. But among 47 trees of all sources that began to flower in the next 3 years, 24 produced only male strobili in their first season, 20 produced only females, and 3 produced both (unpublished data, IFG).

Both kinds of strobili are initiated the season before they emerge from the bud. In shore pine on Vancouver Island, development of the male strobilus and its bud scales began in July and early August (Owens and Molder 1975). By the end of the growing season, microspore mother cells had developed from the sporogenous tissue of the microsporangia (pollen sacs). Female strobili, more distally located on the embryonic shoots, developed later in the season. Bud-scale primordia were laid down by the end of September; and by the time development ceased, about half of the ovuliferous scales had been initiated. In trees of an interior provenance growing in the same environment, these developmental events took place earlier, dormancy was earlier, and the initiation of ovuliferous scales was nearly complete before dormancy.

The initiation of female strobili is influenced by hormones, daylength, and temperature. Gibberellins applied in combination to 4- to 7-year-old seedlings and grafts in Canada significantly increased the proportion of trees producing female cones, but failed to induce male cones (Pharis and others 1975, Wheeler 1979). In Britain, trees grown out-of-doors in containers produced more female cones in short days than in natural daylengths, but in the greenhouse no cones were produced in short days (Longman 1961).

The onset of meiosis in male strobili of trees growing near Stockholm, Sweden, was related to climate at the place of origin, beginning 4 to 5 days earlier in trees from higher latitudes and altitudes (Ekberg and others 1972). The duration of meiosis, from mostly pachytene-diplotene to mostly tetrads, was 3 to 5 days in trees of all sources. Meiosis was more prolonged in south-coastal British Columbia: 8 to 10 days elapsed between pachytene and tetrad stages (Ho and Owens 1974). Some shore pines at Placerville had the most extended period of meiotic activity observed in any pine: 22 days (Saylor and Smith 1966). On these trees, pollen mother cells were dividing at the same time pollen was being shed. Within clusters of male cones, meiosis begins first in the proximal cones, and within single cones, meiosis proceeds from base to tip (Ho and Owens 1974).

Soon after meiosis ends, the development of pollen grains begins with the initiation of wings (sacci) (Ho and Owens 1974). In British Columbia, three mitotic divisions took place within about 1 week, and the pollen grains were mature about 1 week before shedding. At this stage, the male gametophyte consists of generative, tube, and two prothallial cells. In culture, lodgepole pine pollen germinated and completed its development in about 1 week (Ho and Sziklai 1971), a process that takes a year in nature. The fully developed male gametophyte consisted of six cells, nuclei, or cell remnants, including two male nuclei that were either equal or unequal in size.

Pollen-shedding took place 4 to 5 weeks after meiosis in coastal and interior trees growing in coastal British Columbia (Ho and Owens 1974). This interval was shorter in the warmer climate of Placerville, averaging about 3 weeks in a large number of lodgepole pines and hybrids (unpublished data, IFG; L. C. Saylor, pers. commun., 1970).

Lodgepole pine produces unusually large amounts of pollen. Ho and Owens (1973, 1974) estimated the following mean values for the pollen production of shore pines and Montana trees growing in coastal British Columbia:

	Coastal	Interior
Male cones per shoot	15	19.6
Bud scales	7.8	8.3
Microsporophylls per male cone	137.9	93.3
Pollen grains per microsporangium	2,103	2,491
Pollen grains per male-cone cluster	8.9×10^6	9×10^6

Pollen production can be estimated from these data and counts of male-cone clusters produced by young trees at Placerville. At 9 years, 19 Mendocino White Plains trees bore 15,400 clusters of male strobili releasing an estimated 137 billion pollen grains. Only 27 billion grains were produced by 58 coastal trees of the same age. The heaviest individual pollen producer—a White Plains tree about 3 meters tall—produced 2,370 clusters and an estimated 21 billion pollen grains.

In natural stands, pollen is shed between mid-May and mid-July, with coastal trees flowering first (table 1). This sequence is reversed in the common environment of Placerville, where most inland trees flower before coastal trees (Duffield 1953; unpublished data, IFG). In a single season, pollen shedding peaked in this sequence:

Region of origin	Trees	Mean date (May)
Rocky Mountains (eastern B.C. to Colo.)	7	13
Intermountain (southern B.C. to eastern Oreg.)	23	20
Sierra Nevada and Baja California	14	21
Coastal (southern B.C. to Mendocino County, Calif.)	46	26
Mendocino White Plains	26	31

Table 1.—*Time of pollen shedding in natural stands of lodgepole pine*

Locality	Elevation		Years observed	Date of peak shedding	Reference
	Ft	*(m)*			
Vancouver, B.C.	NA[1]		2	Mid- to late May	Ho and Sziklai 1971, Ho and Owens 1974
Northwestern Wash.	500	(150)	10	May 12	[2]
Mendocino White Plains, Calif.	NA		1	June 9	Duffield 1953
Northern Cascades	4,000	(1,200)	NA	Mid-June	Smith 1968
Northern Idaho; western Mont.	NA		10	June 13	[3]
Central and eastern Wash. and Oreg.	2,600-4,250	(800-1,300)	10	June 13	[2]
Southeastern Alberta, "subalpine forest"	NA		NA	June 22	Smithers 1961
Sierra Nevada, Calif.	6,000	(1,970)	3	June 22	Duffield 1953
Central Mont.; Yellowstone region	NA		10	June 25	[3]
Northern Utah	7,200	(2,200)	2	July 12	Krebill 1968
Southern Idaho	6,800	(2,070)	1	July 7	Krebill 1968

[1] NA: not available.

[2] Unpublished data, Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

[3] Unpublished data, Intermt. For. and Range Exp. Stn., Ogden, Utah.

White Plains trees, from two localities about 9 miles (15 km) apart, consistently flowered later than shore pines from the nearby coast. Differences in peak pollen shedding and receptivity of female strobili averaged 7 days in a 3-year period, ranging from 3.7 to 8.9 days.

Jack pine sheds its pollen earlier than lodgepole pine, and their hybrids are intermediate in timing (Duffield 1953, Zavarin and others 1969). In Alberta, jack pines and a putative natural hybrid were shedding pollen on June 2, before lodgepole pines in the vicinity had begun (Moss 1949). At Placerville, pollen shedding followed this sequence in one season:

	Date
Jack pine and offspring of natural hybrids	April 5-12
Backcrosses of artificial hybrids to jack pine	April 4-24
Artificial hybrids (F_1 to F_3)	April 12-27
Lodgepole pine (many sources)	April 21-May 12

The female strobili occur in subterminal or lateral whorls, with one to five strobili per whorl (Black 1961). When both lateral and subterminal strobili are present on the same shoot, the more proximal lateral strobili sometimes develop 2 to 3 days before subterminal strobili (unpublished data, IFG).

Coastal and Mendocino White Plains trees at Placerville tend to be protogynous, although individual trees may be synchronous or protandrous. In a 3-year period, peak female receptivity in these two races preceded peak pollen shedding by a mean of 6.1 days (range 2.3 to 11.2 days). Less complete data for interior sources in the same years suggest that protogyny is not a universal tendency in lodgepole pine. In different years, female flowering peaked 8.5 days earlier, pollen shedding peaked 3.8 days earlier, and the two peaks nearly coincided.

The relative distribution of male and female strobili within the crown was studied in isolated trees and trees in dense stands at 3,300 to 4,900 feet (1,000 to 1,500 m) in the Cascade Mountains of British Columbia (C. C. Smith, pers. commun., Sept. 1976). Females were sometimes restricted to the upper crown, but in most trees—especially isolated ones—they were present through much of the crown. In all trees, the median height of female strobili was in the upper third of the crown. Male strobili were more variable in distribution, with a greater tendency to occur throughout the crown. In most trees, the median height of males was about a third of the distance from the base to the top of the crown; but in a few, the males were concentrated in the upper half of the crown.

From counts of strobili and measures of caloric values of mature male and female cones, Smith estimated the relative energy invested in male and female reproductive structures. The ratio of female to male energy investment ranged from 16.4 for trees in a recently thinned stand to 0.5 for isolated trees. In dense stands of varying age, these values tended to approach unity, ranging from 1.2 to 2.1. The estimated gametophytic sex ratio was 5.5×10^6: for each potentially functional female gametophyte, lodgepole pine produced 5.5 million pollen grains (C. C. Smith, pers. commun., Sept. 1976).

Coastal and Mendocino White Plains trees at Placerville differ not only in the absolute quantity of pollen produced, but in the relative investment in the sexes. In coastal trees, the ratio between number of male-cone clusters and number of female strobili was 0.7, 0.9, and 1.6 at ages 7, 8 and 9. White Plains trees had ratios of 4.9, 9.8, and 21.4. This difference was a general property of the two races: at age 9, 14 of 19 White Plains trees, but only 4 of 58 coastal trees, produced more than 200 clusters of male strobili. This heavy investment in pollen production is also characteristic of older White Plains trees growing in nature. From Westman and Whittaker's (1975) estimates of reproductive biomass and Ho and Owens' (1974) counts of male cones per cluster, the average ratio between numbers of male-cone clusters and individual female strobili can be estimated at 22.6 in trees 15 to 92 years old.

Fertilization takes place a year or more after pollination, in June (Chamberlain 1935) or July (Buchholz 1945). In a lodgepole pine growing at 1,740 meters in the Sierra Nevada, fertilization took place between July 10 and 12 in strobili pollinated on June 29 and July 1 of the year before (Buchholz 1945; unpublished data, IFG). The apical meristem and cotyledon primordia of the embryo differentiated in mid-August, and the embryo reached nearly full size about a month before seed shed.

In the far north, embryo development may be adversely affected by climate. As much as a third of the seeds from trees in the Yukon had small, poorly developed embryos—much higher levels than trees in southern British Columbia (O. Sziklai, pers. commun., Oct. 1975), and germination of IUFRO (International Union of Forest Research Organizations) seed lots from the Yukon was mostly less than 50 percent (R. Lines, pers. commun., June 1978).

Abnormal reproductive structures are fairly common in lodgepole pine, and have been noted more often on trees from interior sources than on coastal trees in Britain (Black 1961), British Columbia (Ho and Owens 1974), and at Placerville (unpublished data, IFG). Female strobili may replace all or part of the male strobili in a cluster (Black 1961; unpublished data, IFG), and male strobili occasionally replace female strobili (unpublished data, IFG). Rarely, male strobili replace terminal buds (Black 1961, Ho and Owens 1973). Bisexual cones may have male appendages at the base and female above (Black 1961) or the reverse arrangement (unpublished data, IFG). Other reproductive deviations are microsporophylls with 1, 3, and 4 microsporangia, and pollen grains with 3 to 5 wings (Ho and Owens 1974).

Cone and Seed Production

Although the retention of seed in serotinous cones is a distinctive feature of some races of lodgepole pine, even stands with the highest frequencies of closed cones produce some cones that open at maturity. The timing of cone opening does not show consistent geographic trends, but it is tardy and erratic in coastal stands. In northwestern Washington at 500 feet (150 m), the 10-year mean date of cone-opening was September 20 (data on file, Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.). In central and eastern Oregon and Washington at 2,600 to 4,250 feet (800 to 1,300 m), 10-year means range from August 31 to October 1. The peak of cone-opening is about September 5 in northern Idaho, Montana, and the Yellowstone region, ranging from late August to the end of October (data on file, Intermt. For. and Range Exp. Stn., Ogden, Utah). At elevations of 4,900 to 7,900 feet (1,500 to 2,400 m) in the central Sierra Nevada, cones open between September 20 and October 20, peaking in the first half of October (unpublished data, IFG). In south-central Oregon, 80 percent of the seed was shed by early November over a 15-year period (Dahms and Barrett 1975). Shedding was slightly later at higher elevations (Mowat 1960). In the subalpine forest of Alberta, seed shedding reached its peak between the last week in September and the middle of October in 3 successive years, beginning in early September and tapering off as late as November (Crossley 1955a).

In many stands, much of the annual seed crop remains on the trees in cones that remain closed indefinitely. Most mature trees have either predominantly (>90 percent) closed or predominantly open cones. The frequency of trees with mostly closed cones ranges from 0 to nearly 100 percent, varying with stand and region. Most coastal stands produce only open cones. Illingworth (1970) found a single closed-cone tree among several thousand on the coastal islands of British Columbia. Trees with closed cones were more common in small stands at fjord heads and in major river valleys cutting through the Coast Mountains of British Columbia and Alaska. Illingworth found up to 10 percent closed-cone trees in these stands, but along the major valleys open cones tended to predominate far inland. At the head of the Lynn Canal, a fjord on the Alaska coast, stands with closed cones are common, and Viereck and Little (1972) described them as a localized coastward extension of interior variety *latifolia*. Closed-cone trees are also present at low frequencies in some stands near the head of the Hood Canal in the Puget Sound region, Washington (B. C. Wilson, pers. commun., Aug. 1977). Closed cones are common in the Del Norte race of northwestern California, isolated from open-cone populations to the west and east. Closed cones are also common in the pygmy forest of the Mendocino White Plains, which is contiguous with the open-cone population along the nearby coastline. On the White Plains, dwarfed trees 15 to 92 years old averaged about 32 percent closed cones (Westman and Whittaker 1975).

Serotinous cones are unknown in the Sierra Nevada and the mountains of southern and Baja California (Critchfield 1957) and in the southern Cascades at least as far north as central Oregon (Mowat 1960). To the north and east, trees with closed cones increase in frequency. They are rare in the Columbia River region (Critchfield 1957), occasional in the mountains of eastern Oregon (Trappe and Harris 1958) and central Idaho (Lotan 1975a), and common at the northern end of the

Cascades in southwestern British Columbia (Smith 1968) and in the Salmon River Mountains of north-central Idaho (Lotan 1975a).

The frequency of closed-cone trees in mature stands is highly variable in the Rocky Mountain-Intermountain region. East of the Coast Mountains, most stands in interior British Columbia are predominantly serotinous, with less than 10 percent open-cone trees (Illingworth 1970). This percentage decreases still further in northeastern British Columbia and the Yukon. Open-cone trees are more common in the interior wet belt of southeastern British Columbia—60 to 70 percent in some stands (Illingworth 1970)—and are predominant across the border at low elevations in northeastern Washington and northern Idaho (Lotan 1970, 1975a). Many stands in northwestern Wyoming also have a high frequency of open-cone trees—100 percent in some localities (Lotan 1975a).

The frequency of closed cones increases with tree age. In eastern Idaho, Mason (1915) estimated that five-sixths of the cones open at maturity in stands less than 55 years old, but in older stands only one-quarter of the cones open. This age relationship was confirmed by Crossley (1956a) in Alberta and Armit (1964) in British Columbia. In Alberta, closed-cone trees increased from 17 percent in 17-year-old stands to more than 80 percent in stands 55 years or older. Open-cone trees correspondingly decreased from 66 to 8 percent, with the remainder in the intermediate range. In north-central British Columbia, a small sample of trees less than 25 years old included 86 percent open-cone and no closed-cone trees, but 88 percent of trees more than 60 years old had closed cones and only 4 percent had open cones. Rough estimates of the age at which this reversal takes place range from 17 to 55 years in Alberta (Crossley 1956a) and 25 to 60 years in British Columbia (Armit 1964) to 20 to 30 years in Montana (Lotan 1975a).

Except for tree age, the factors influencing the occurrence of closed cones are obscure. The importance of stand fire history is widely assumed, but supporting evidence is sparse. Lotan (1967a) found more closed-cone trees (58 percent) in an even-aged stand on an old burn than in an all-aged stand on a nearby alluvial flat (38 percent). The frequency of closed-cone trees did not appear to be closely related to habitat type in the northern Rocky Mountains (Lotan 1975a), but many stands with more than 50 percent closed-cone trees were in *Abies lasiocarpa* habitat types of the lower subalpine zone. In the Bitterroot Mountains of Montana, this zone may be more prone to high-intensity fires than forest zones below or above it (Arno 1976). A general relationship between the successional status of lodgepole pine and the frequency of closed cones was suggested by Hoffman and Alexander (1976) in their survey of habitat types in the Bighorn Mountains, Wyoming. In communities where lodgepole pine was the dominant climax species, it tended to have a high proportion of open cones; but where the species was successional, closed cones were more common.

Cone serotiny is related to elevation in some places but not in others. In Alberta, Crossley (1956a) found an increase from 45 to 95 percent in the frequency of open-cone trees as elevation increased from 4,800 to 5,700 feet (1,460 to 1,740 m). Illingworth (1970) also noted an elevational gradient in British Columbia, with open-cone trees sometimes predominant in semi-alpine stands. Critchfield (1957) observed a corresponding decrease with elevation in the related character of cone density and speculated that both characteristics might be related to elevation throughout the Rocky Mountain region. Lotan's (1975a) extensive observations, however, established that the frequency of closed-cone trees does not always decrease with elevation. Almost none of the variation in parts of western Montana was related to elevation. In northwestern Washington, where a close relationship did exist, the percentage of trees with serotinous cones *increased* from 10 to more than 80 between low- and high-elevation forest types.

In all Rocky Mountain stands that have been looked at in detail, trees with predominantly closed or open cones greatly outnumber intermediates (trees with 10 to 90 percent closed or open cones) (table 2). The inheritance of the closed-cone trait has not been studied in lodgepole pine, but this distribution of phenotypes led Crossley (1956a), Lotan (1967a), and others to infer that this trait is highly heritable. In jack pine, Rudolph and others (1959) concluded, from observations of 17- and 18-year-old wind-pollinated progenies of trees with known phenotypes, that cone serotiny is under strong genetic control—probably by more than one gene. One problem in interpreting their data is that the frequency of closed cones increases with tree age in jack pine (Jameson 1961), as it does in lodgepole pine, and the trees they studied may have been too young for the full expression of this trait. These and other data on jack pine, as well as Lotan's (1967a) data on lodgepole pine, were reinterpreted by Teich (1970) in terms of a single additive gene with two alleles. Consistently deficient numbers of intermediates (Teich's heterozygous class) were attributed either to misclassification of phenotypes or to a high level of inbreeding. Large-scale misclassification is not supported by the clustering of 80 to 90 percent of all trees at the two extremes of expression (table 2), and the estimated degree of inbreeding is an order of magnitude greater than other estimates for pines. Alternative genetic models based on a single gene with dominance and variable expressivity, or on more than one locus, are in better agreement with the data. However, the low frequency or absence of closed-cone trees in many stands established after fire led Lotan (1976) to express doubts about a simple genetic model.

Although the inheritance of the closed-cone habit is poorly understood, differences between natural populations tend to be retained in the common environment of Placerville. Most conspicuous is the contrast between the serotinous Mendocino White Plains race and trees from a nearby open-cone coastal stand. Recent cone crops on all 23-year-old trees from the White Plains were serotinous to varying degrees, but the cones on coastal trees all opened by the spring following maturation. A few trees of other coastal origins (Oregon, Vancouver Island) had low or moderate numbers of closed cones, unlike their open-cone parents in nature. At this age, Rocky Mountain trees were beginning to segregate into two groups with mostly open or mostly closed cones.

The scales of lodgepole cones are bonded together at their tips by resin, and open- and closed-cone trees may differ in the temperature required to melt the resin. Serotinous cones collected in Colorado required temperatures of 45° to 50° C to melt the resin and allow the scales to separate (Clements 1910). Cameron (1953) determined that the bonded scales of serotinous lodgepole cones separated in a water bath at 45.3° C and that the extracted resin had a melting point of 45.5° C, compared with 50° C for jack pine. Armit (1964) observed a broad range of cone-opening temperatures in interior British Columbia, with most serotinous cones opening at 45° to 47° C but the cones of some trees requiring temperatures of 51° to 54° C. Perry and Lotan (1977) also observed marked differences in a 14-tree sample of (1) open-cone, (2) intermediate, and (3) closed-cone trees in Washington, Idaho, and Montana. Temperatures required for 90 percent cone opening were: (1) 42° to 45° C, (2) 41° to 47° C, and (3) 47° to 59° C. The range of temperatures at which the cones opened was also highly variable, with some trees having a fairly specific threshold and the cones of others opening through a broad range of temperatures. Old cones opened at higher or lower temperatures than newly matured cones, depending on the tree.

Melting of the bonding resin can be achieved by a brief immersion in boiling water or, as Lotan (1975a) recommended, a 5- to 10-minute immersion in hot water (60° C). Once the seal is broken, the scales separate and release the seed after a

Table 2.—*Incidence of closed- and open-cone trees in mature stands of lodgepole pine*

Location	Age	Closed	Intermediate	Open	Reference
	Years		*Percent*		
1. Alberta, subalpine zone	55	82	10	8	Crossley 1956a
2. Same as 1	140-250	83	17	0	Crossley 1956a
3. North-central B.C.	60-120 +	88	8	4	Armit 1964
Southern Mont.:					
4. Alluvial flat	40-230	38	14	48	Lotan 1967a
5. Old burn (near 4)	88	58	10	32	Lotan 1967a
Eastern Idaho:					
6. 6,500 ft	117	48	19	33	Lotan 1968
7. 7,700 ft	191	23	20	57	Lotan 1968

12-hour exposure to a drying temperature of 60° C. Temperatures much higher than this (66° C or more) reduce germination (Lotan 1975a).

It has not been satisfactorily established to what extent serotinous cones open on the tree in the absence of fire. Clements (1910) described two periods of cone opening in Colorado: the first few years and 10 to 13 years after cone maturation. He suggested that the second period was related to the drying of cones following the rupture of the vascular connection in the cone pedicel. His observations have not been confirmed by later work in the northern Rocky Mountains, but the discrepancies could reflect regional differences in cone-opening behavior. Neither Crossley (1956a) nor Lotan (1975a) observed Clements' second period of cone opening. Celements' suggested mechanism is not in agreement with Beaufait's (1960) finding that serotinous cones of jack pine do not receive moisture from the tree, but are in equilibrium moisture content with the environment.

From an analysis of the entire cone complement of individual trees in Alberta, Crossley (1956a) concluded that lodgepole cones either open promptly at maturity or stay closed indefinitely in the absence of fire. Armit (1968), however, observed an unusually heavy seed fall in interior British Columbia—up to three times the estimated current crop—after an extended period of unusually hot (> 80° F) dry weather in late summer. He attributed it to the opening of old cones. He considered 80° F (26.5° C) sufficient to raise the cone surface temperature to 51.5° C and cause the resin seal to rupture. Crossley (1956a) concluded the opposite: that temperatures of 45° C or more do not ordinarily occur in tree crowns. In a companion paper, however, Crossley (1956b) observed that detached cones exposed to direct sunlight opened after reaching surface temperatures of 42° to 47.5° C. Ackerman (1966) found that old weathered cones on Alberta trees had higher surface temperatures—and opened more often on the tree—than young unweathered cones.

In regions where the maintenance of a reserve seed supply in closed cones is of overriding selective importance, lodgepole pine has evolved secondary adaptations to minimize depredations by tree squirrels *(Tamiasciurus)*. The squirrels extract seed more efficiently from ripening cones, but older serotinous cones provide a food supply of last resort (Smith 1970). The red squirrel *(T. hudsonicus)* is present throughout the closed-cone interior region. It is better adapted to extracting seed from serotinous cones than the Douglas squirrel *(T. douglasii)*, which replaces it through most of the open-cone coastal and Sierra-Cascade regions. Smith (1970) and Elliott (1974) described a variety of ways in which closed-cone trees minimize seed losses to tree squirrels. Better adapted cones occur in whorls; are flush with the branch; are wider and stouter; and have large, hard, basal apophyses. They contain fewer seeds and invest a high percentage of energy in woody protective tissue. In the northern Cascades and Colorado, only 1.9 to 2.0 percent of total cone energy is in the seeds, compared with 7 to 29 percent in non-serotinous conifers of the same regions (spruce, fir, Douglas-fir, ponderosa pine).

Much of the seed in serotinous cones retains its viability for many years. Germination of seed from old cones collected in Idaho and Colorado was highly variable in Clements' (1910) study, but in a decade-long, large-scale study in southern Wyoming and Colorado, seed from closed cones of all ages averaged 91 to 92 percent of fresh-seed germination (Bates 1930). In eastern Oregon, 50 to 70 percent of the seed from 15- and 30-year-old cones was germinable (Trappe and Harris 1958). Montana seed from cones 20 to 36 years old had a germinative capacity of 40 to 50 percent (Lotan 1970). Seed from cones of all ages in western Alberta was more than 90 percent germinable (Ackerman 1966). Seed from serotinous cones collected in the Cypress Hills of Saskatchewan and stored for 20 years in circumstances simulating natural conditions was 80 to 92 percent germinable (Crossley 1955b). Clements (1910) germinated a few seeds from cones 45 and 75 to 80 years old, but the record for seed longevity in lodgepole pine appears to be three germinable seeds obtained from 150-year-old cones that had been overgrown and imbedded in the heart of a 182-year-old Colorado tree (Mills 1915, p. 223).

Jack pine seed survives brief exposures to extremely high temperatures (Beaufait 1960), and this finding may also apply to lodgepole pine. The seed in serotinous jack pine cones suffered no loss in viability after the cones were exposed to 700° F (371° C) for up to 2 minutes. Extracted seed withstood exposure to the same temperature for up to 10 seconds without loss of viability.

Most estimates of the number of sound or germinable seeds in a lodgepole cone fall short of the early approximations of 26 and 40 seeds per cone in the southern Rocky Mountains (Mason 1915, Bates 1930). In the same region, a 10-tree sample averaged only 20.3 sound seeds per cone, with the largest cones averaging 43 to 46 seeds (Clements 1910). Stand means in southern Montana and eastern Idaho were 10.7 to 21.1 sound seeds per cone (Lotan 1967a, 1968). In three western Alberta stands, the average number of viable seeds per cone was 14.6 to 18.5 (Ackerman 1966). In the northern Cascades, cones averaged 14.8 sound seeds in one season (Smith 1968), but the next year tree-means were 15.3 to 44.8 sound seeds per cone (Smith 1970). A large number of trees in the central Sierra Nevada had a median of 16 sound seeds per cone and a range of 5 to 37 (unpublished data, IFG).

Estimates of the proportion of sound seed are fairly consistent from region to region. Sierra Nevada seed averaged 71.6 percent sound, with tree means of 34 to 93 percent. Seed caught in traps at two Oregon sites averaged 74.7 and 79.3 percent sound (Dahms and Barrett 1975). Soundness ranged from 20 to 40 percent in poor seed years to a maximum of 85 to 87 percent in good years. In Colorado stands with differing frequencies of lodgepole pine, the proportion of filled seeds increased from 65 to 88 percent as lodgepole pine increased in importance (C. C. Smith, pers. commun., Sept. 1976), but a simple interpretation of increasing pollen availability is complicated by the greater likelihood of selfing (and more hollow seeds) in stands with fewer lodgepole pines.

One reason for the generally high proportion of sound seed may be the relative freedom of lodgepole pine from cone and seed insects (Keen 1958, Lavender 1978, Smith 1968). One locally damaging insect is the lodgepole cone moth (*Eucosma rescissoriana*), whose larvae may cause significant damage to second-year cones of inland populations (Hedlin 1974, Keen 1958, Lavender 1978).

Lodgepole pine is a more reliable seed producer than its tree associates in Montana (Boe 1954), Colorado (Bates 1930), and southern Oregon (Dahms and Barrett 1975). No crop failures were observed during 10- to 20-year periods in Alberta (Crossley 1956a), western Colorado (Bates 1930), and two sites in southern Oregon (Dahms and Barrett 1975). A single complete failure in a southern Wyoming stand in a 10-year period was attributed to unusually low temperatures (– 8° C) at the end of June in the preceding season (Bates 1930).

Large quantities of seed are produced in most stands. Seed production was comparatively light in a southern Wyoming stand, averaging 180,000 germinable seed per hectare annually, with a range of 0 to 336,000 over a 10-year period (Bates 1930). A Colorado stand was more productive, averaging 790,000 germinable seed per hectare (range: 74,000 to 2,042,000) In one season, the lodgepole pines comprising 40 percent of a north Cascades stand produced 657,000 sound seeds per hectare (Smith 1968). Two nearly pure stands in south-central Oregon averaged 714,000 and 701,000 sound seeds per hectare annually over periods of 16 and 11 years, ranging from about 12,000 to 2,223,000 (Dahms and Barrett 1975). No periodicity was found in any of these studies: the four largest crops in Colorado and the two largest in Wyoming were produced in successive years (Bates 1930).

In stands where closed cones are common, most of the seed crop is added to the reserve supply, and the annual seed fall is small: 25,000 to 71,000 sound seeds per hectare in Alberta over a 3-year period (Crossley 1955a) and an average of 43,000 per hectare in Montana in a 4-year period (Boe 1956). Small amounts of seed were shed almost year-round in both regions, and it is uncertain whether a small summer peak in Alberta was due to the occasional opening of old closed cones or the more complete opening of partly open cones.

The reserve supply of seeds in serotinous cones may be very large (table 3), depending on stand age and composition, frequency of closed-cone trees, squirrel predation, and other factors. Estimates range from about half of the annual crop in the northern Cascades (Smith 1968) to 2.5 to 3.5 times the annual crop in the southern Rocky Mountains (Bates 1930).

Lodgepole and jack pines have the smallest seeds of any of the pines (Uyeki 1927). Published 1,000-seed weights provide a fairly consistent picture of this variable character in lodgepole pine (Maschning 1971, Hagner and Fahlroth 1974,

Table 3—*Amount of seed stored in closed cones of lodgepole pine stands*

Region	Stored seed Sound	 Germinable	Reference
	1,000/ha		
Western Alberta (17-year-old stand)	111		Crossley 1956a
Western Alberta (mature stands)		3,700-6,000	Ackerman 1966
Northern Cascades (mixed stand)	330		Smith 1968
Southern Wyoming		447	Bates 1930
Western Colorado		2,700	Bates 1930
Southern Montana, eastern Idaho (stands 4 to 7, table 2)	2,000-7,900		Lotan 1967a, 1968

Birot 1978). Seed weight increases sharply from north to south along the coast from Vancouver Island-Puget Sound (2.5 to 3.5 mg per seed) to southern Oregon and northern California (4.8 to 6.1 mg), and in the interior from eastern Oregon (3.8 to 5.3 mg) to the California mountains (5.2 to 11.4 mg) (Maschning 1971, Birot 1978). These steep north-south gradients may reflect adaptation to the summer-dry climate of California, where Baker (1972) found a positive relationship between seed weight and increasing environmental aridity. Farther north, this apparent correlation with latitude disappears: IUFRO collections from Vancouver Island and southeastern Alaska have mean seed weights of 3.1 and 3.3 milligrams (Birot 1978). In the interior of Canada, seed weight is low and rather uniform (2.3 to 3.5 mg) throughout British Columbia and the Yukon (Birot 1978; data of Hagner and Fahlroth 1974, corrected for empty seeds). Farther east and south, in Alberta and the American Rocky Mountains, seed weight is greater (2.8 to 5.6 mg), but the available data does not suggest a north-south trend (Maschning 1971; Birot 1978; H. Barner, pers. commun., Jan. 1979). Among the IUFRO collections from the Rocky Mountain-Intermountain region, the heaviest seed (5.6 mg) was from the Cypress Hills, Alberta (Birot 1978).

The energy invested in Colorado seeds is partitioned as follows (Smith 1970):

	Percent
Endosperm plus embryo	77.6
Seed coat	13.7
Wing	8.8

Mean cotyledon number is closely related to seed weight but much less variable (Maschning 1971). Nearly all California montane samples had significantly higher average numbers (4.7 to 5.4) than samples from coastal and Rocky Mountain-Intermountain regions (3.4 to 4.3 and 3.5 to 4.8). Cotyledons of individual seedlings number 2 to 9.

The small seeds of lodgepole pine are among the most dispersible of any North American conifer seeds. Under ordinary forest conditions, most seed falls to the ground within 200 feet (60 m) of the source (Lotan 1975b, Dahms and Barrett 1975), although Crossley (1955a) found no significant difference between the seed catch near a stand edge and 100 meters from the edge. In some conditions, the seeds are highly mobile owing to their slow rate of fall. Terminal velocity is 0.6 to 0.8 meter per second (Siggins 1933, Cremer 1971), a slower rate of fall than that of almost any other western conifer seed (Siggins 1933). Cremer (1971) estimated dispersal distances of 214, 168 to 223, and 336 meters for seeds of Monterey pine, Douglas-fir, and lodgepole pine released 30 meters above the ground in a 15-mile-per-hour wind. Cremer saw updrafts catch lodgepole pine seeds and move them upward and out of sight, and Siggins made the same observation with Sitka spruce and incense-cedar seed, both having greater terminal velocities than lodgepole seeds. Sometimes seed is carried for long distances by the wind; trees have become established 10 to 11 miles (16 to 18 km) from their parents in New Zealand (Bannister 1965). Lotan (1976) noted lodgepole seed scudding over crusted snow, and suggested that seed might be dispersed for considerable distances in this way.

Self- and Cross-pollination

Among the pines, lodgepole pine may be one of the most difficult to self. Ten coastal and Mendocino White Plains trees with fair seed yields from outcrosses (> 5 sound seeds per cone) produced few sound seeds when they were selfed at Placerville. Selfing produced nearly the same yield of cones from pollinated strobili as outcrossing (68 and 68.5 percent) and almost the same total number of seeds per cone (18.6 and 18.0), but few seeds were filled. Selfing ability (sound seed from selfing as a percent of sound seed from outcrossing) averaged 16 percent, ranging from 0 to

57 percent. Two Sierra Nevada trees in different stands gave similar results: about the same total number of seeds per cone from selfs and outcrosses (14.3 and 15.8) but low selfing ability (12.3 and 7.0 percent).

Genetic barriers to selfing are apparently expressed after fertilization in lodgepole pine, as they are in other pines (Franklin 1970). This conclusion is based on (1) equal yields of cones and seed coats from selfing and outcrossing, and (2) Hagman's (1967) observation that there is no barrier to pollen tube growth after self-pollination of interior lodgepole pine in Finland. The low estimate of selfing ability for lodgepole pine—about 16 percent for all crosses—places it near the lower end of the range among pine species, which average 66 percent (Franklin 1970).

Controlled Pollination

Standard techniques described by Cumming and Righter (1948) are applicable to lodgepole pine, except that heavyweight pollination bags are unsuited to the relatively slender branches of this species. The kraft paper bags used in maize breeding were successfully utilized by Sorensen and Miles (1974), who found that bagged and unbagged strobili suffered about the same amount of freezing damage.

A single gram of lodgepole pine pollen comprises about 33.5 million grains (Ho and Owens 1974). Germination of pollen in distilled water is not improved by the addition of sucrose, hormones, or other compounds (Ho and Sziklai 1971) and is not much affected by storage for 1 to 2 years at temperatures of 4° C or −18° C (Ehrenberg 1960). The results of *in vitro* germination tests, however, bear little relation to the ability of the pollen to function *in vivo*. In a preliminary report of a long-term study of pollen storage at Placerville, Callaham and Steinhoff (1966) corroborated Ehrenberg's finding that storing lodgepole pollen for 1 year at about 5° C had little effect on *in vitro* germination, but the pollen had lost much of its ability to function in reproduction. A total of nine crosses were made on three Sierra Nevada trees with pollen from three trees in another stand. Crosses with refrigerated pollen produced only 44 percent as many cones, 52 percent as many total seeds, and 18 percent as many sound seeds as crosses with fresh pollen. After 2 years of refrigeration, crosses with the same pollens produced few cones and seed coats, and no sound seeds.

In contrast to refrigeration, storage for a year in a domestic deep-freezer at about −20° C is highly effective in preserving the ability of the pollen to function *in vivo*, and fresh and 1-year-old frozen pollen are used almost interchangeably in breeding at Placerville. Like some other species in the pollen storage study, lodgepole pine unexplainably produced more sound seeds with pollen frozen for 1 year than with fresh pollen (table 4). After 3 and 5 years of storage, crosses with frozen pollen produced only about half as many sound seeds as the controls. In subsequent years, cone and seed yields fell off rapidly.

Table 4.—*Cone and seed yields from crosses with deep-frozen lodgepole pine pollen*[1]

Years in freezer	Strobili yielding cones	Total seed per cone	Sound seed per cone
	Percent		
1	100	161	131
3	76	59	46
5	96	57	49
8	86	37	20
11	36	16	3
15	0		

[1] Unpublished data, IFG. Values expressed as percentage of fresh-pollen controls.

A minimum number of viable ovules are needed to sustain cone development in *P. sylvestris* (Sarvas 1962). By 11 years, lodgepole pine may have fallen below this threshold: cone yield dropped from 86 to 36 percent of the controls between 8 and 11 years.

A high proportion of control-pollinated female strobili develops into cones in Sierra Nevada lodgepole pine. In the three trees used in the pollen-storage study at Placerville, each pollinated with fresh pollen in six seasons, 61 percent of all pollinated strobili developed into cones. Tree means were 46 to 68 percent, and annual means 49 to 79 percent. The yield of cones from

2,500 strobili on five trees in another stand, pollinated with a variety of pollens, averaged 70 percent over two to five seasons, with tree means of 57 to 80 percent.

The yield of sound seeds from control-pollinated cones may be a little higher than that of wind-pollinated cones, The median yield of three trees control-pollinated in six seasons was 18.2 sound and 26.4 total seeds per cone, compared with 16.0 and 26.1 for a large number of wind-pollinated cones from other trees. Maximum seed production of the three trees was 50 to 58 sound seeds per cone. The percentage of sound seeds per cone for individual crosses was 64.9 to 92.9, and seasonal means were 63 to 86.5 percent.

Germination and Establishment

Lodgepole pine seed has no absolute stratification requirement for germination, but seed stratified for as little as 2 weeks germinates faster than untreated seed (Critchfield 1957, Roche 1962). Stratification for 4 weeks is recommended in Britain (Forestry Commission 1976), but in an Alberta nursery unstratified seed from several sources produced significantly larger numbers of 1st-year seedlings than stratified seed (Hocking 1972).

Germination of unstratified seed is under fairly strict temperature control. At optimum temperatures the seed germinates rapidly and almost completely. In 7-day tests, germination of fresh seed from several stands at 400 to 1,500 meters in south-central British Columbia was 76 to 90 percent at 24° C and 27° C, peaking at 4 to 5 and 3 days (Haasis and Thrupp 1931). At higher (33° to 41° C) and lower (15°, 19° C) temperatures, both the amount and speed of germination decreased, but low-elevation seed germinated relatively better at high temperatures and high-elevation seed at low temperatures. Fresh seed from 1,400 meters in Alberta showed 88 to 94 percent germination in 13-day tests at a constant temperature of 21° C and at fluctuating temperature regimes in the same range, decreasing at higher (27°, 32°C) and lower (16°C) constant temperatures (Ackerman and Farrar 1965). At optimum temperatures, germination peaked at 4 to 7 days. Germination of seed from 9,800 feet (3,000 m) in Colorado peaked at about the same time in 3-week tests at 25° C, with total germination of 75 to 90 percent (Kaufman and Eckard 1977). At 16° C germination was slower and nearly as complete, but at lower (12° C) and higher (35° C) temperatures total germination decreased. Old seed germinates about as fast as fresh seed: 19- to 20-year-old seed from the Cypress Hills peaked in 7 days or less (Crossley 1955b), and seed from 6-year-old logging slash at 3000 meters in Utah peaked at 8 days (Tackle 1954). Southern Rocky Mountain seed covered by about 6 millimeters of sand had germination peaks at 11 to 15 days (Bates 1930). Recent information provides no support for the conclusion of Bates and others (1929) that germination is prompt and complete only with fluctuating temperatures, nor for Bates's (1930) statement that germination is often delayed until a year after planting.

Germination of seed from coastal stands is slower than that of seed from the Rocky Mountain-Intermountain region (Rafn 1915, Critchfield 1957, Roche 1962, Forestry Commission 1970). Stratification does not eliminate this difference. In Roche's tests at 25° C, median germination time of coastal seed was about twice that of interior seed (Canadian sources), whether the seed was unstratified (germination times 10 to 11 and 5 days) or stratified for 6 weeks (2.5 to 3.5 and 1.5 days). In tests at 20° C with seed that had been stratified and air-dried (a treatment that largely reversed the effect of stratification), mean germination rates were 8 to 19 days in coastal and 4.5 to 8.6 days in Rocky Mountain-Intermountain samples (Critchfield 1957). At a higher temperature (30° C), the germination behavior of coastal seed was relatively unchanged, but the interior sources were significantly more variable in germination speed. A temperature of 10° C was suboptimal for both groups; amount of germination was reduced to 20 to 25 percent of that at 20° C, and mean germination time was extended to 55 to 65 days for coastal seed and 22 to 34 days for Rocky Mountain-Intermountain seed. In contrast, germination of small samples of Sierra Nevada seed at 10° C was also slow (mean 48 days), but nearly complete (85 percent of germination at 20° C).

Both lodgepole and jack pine seed require exposure to light for germination, but lodgepole pine is much more exacting in both light and temperature requirements (Ackerman and Farrar 1965). Jack pine seed above a threshold moisture content germinated completely at a wide range of temperatures after a few minutes exposure to light, but complete germination of Alberta lodgepole seed required repeated long exposures or continuous light.

Germination of Colorado lodgepole seed was delayed and reduced by even a thin (1 to 3 mm) covering of soil, but moderate water stress did not greatly influence the amount of germination (Kaufman and Eckard 1977). Germination of south-central Oregon seed was not much reduced by levels of soil water sufficiently high to substantially depress the germination of ponderosa pine (Cochran 1972).

In natural conditions, lodgepole seed germinates at temperatures far below the optimum range for unstratified seed in the laboratory. Germination took place during the second week in May in southern Oregon, at a time when freezing night temperatures were still common (Cochran and Berntsen 1973). In the Yellowstone region at 7,800 feet (2,380 m), seed sown the previous October germinated at the end of June and beginning of July, soon after the snow melted (Lotan 1964). One explanation for this discrepancy is that natural conditions simulate artificial stratification, and the temperature requirements for germination of stratified seed have not been investigated.

Newly germinated seedlings are relatively insensitive to temperature extremes. In south-central Oregon they suffered little mortality at freezing temperatures above −6.5° C (Cochran and Berntsen 1973). At lower temperatures, mortality increased with seedling age. At −10.5° C, 1-week-old seedlings had low mortality, but 2-month-old seedlings were all killed. On these pumice soils, drought, heat, and frost-heaving all contribute to seedling mortality (Cochran 1973, 1975). Near Yellowstone, 90 percent of seedling mortality was attributed to drought. Soil-surface temperatures exceeding 138° F (59° C) were not an important factor (Lotan 1964).

In regions where closed cones are common, stands established after forest fires are often tremendously overstocked (Mason 1915, Horton 1956). Referring to northern Rocky Mountain stands, Smithers (1961) stated, "It is doubtful if any other species can demonstrate such high levels of stocking." Less extreme overstocking is also common after logging. In Alberta, most seedlings became established in the first 3 to 6 years after a fire (Horton 1953) and the first 8 to 10 years after clearcutting and site scarification (Crossley 1976, Johnstone 1976). Clements (1910) attributed the heavy reproduction on old burns to the temporary absence of seed predators like chipmunks and squirrels after a fire. The density of stands on old burns suggests that individual lodgepole pines have a greater chance of surviving to reproductive age than individuals of associated tree species.

Vegetative Propagation

Grafting

Grafting out-of-doors gave poor results in Ireland (O'Driscoll 1972) and is done indoors there and in Great Britain (A. M. Fletcher, pers. commun., Jan 1972). In south-central Oregon, outdoor grafting on native seedlings has been done on a large scale in the spring (Copes 1975). The grafted trees are dug up immediately and planted in containers, where they remain for 2 to 3 years. Scots pine was successfully used as a rootstock for interior lodgepole pine in eastern Canada, but growth was not entirely satisfactory (Holst and others 1956). The same species has also been used as a rootstock in Great Britain, but south-coastal lodgepole pine is preferred (A. M. Fletcher, pers. commun., Jan. 1972). Rootstocks are taken indoors in January, and grafting is done just before the buds flush. The preferred method is an apical side-veneer graft, with a small branch left on the rootstock; but depending on the size of stock and scion, ordinary side-veneer grafts are also used. Top-cleft grafts are used in Oregon (Copes 1975). Grafting success depends partly on the clone, and in Ireland grafting success was 38 to 84 percent over a 5-year period, averaging 65 percent. Percent success is comparable in Britain (Forestry Commission 1972), but many clones give in excess of 75 percent successful grafts. The grafts are planted in the nursery during the following season, and culled heavily before outplanting 2 years after grafting (A. M. Fletcher, pers. commun., Jan. 1972). One problem in Britain is obtaining vegetative shoots from older trees on which nearly all the shoots bear male-strobilus buds.

In British Columbia, survival of 2-year-old grafts was 78 percent; but in a few clones, grafting failures reached 70 percent (Illingworth 1975). In one breeding arboretum, more than 40 percent of the clones produced female strobili 1 year after outplanting and 2 years after grafting (Wheeler 1979). Flowering was much more common on ramets grafted onto field-grown stock than on grafts using potted stock.

Delayed graft incompatibility has not been reported in lodgepole pine. Incompatibility shows up soon after grafting in Ireland (O'Driscoll 1972). In New Zealand, grafts are rogued at the end of the first year (Copes 1975). In Oregon, about 10 percent of the grafts show external symptoms of incompatibility—scion overgrowth and chlorotic needles—within 2 to 3 years, and roguing is done then (Copes 1975). Copes found only limited xylem growth in the region of the graft union of incompatible grafts.

Rooting

Lodgepole pine cuttings are moderately easy to root. Working in Britain with coastal trees 3 to 35 years old, Iktüeren (1973) found a decline in rootability between 3 and 19 years, but in other studies tree age does not appear to be as influential as it is in many other pines. Cuttings taken in December from 2-year-old Oregon seedlings rooted poorly under optimum conditions: hormone treatment, frequent application of nutrients and fungicides, and a rooting-medium temperature of 27° C (Morden and Ross 1976). The cuttings did not begin to callus until the 7th week, and after 4 months only 40 percent had rooted. Better success has been reported in other tests involving older trees. In California, cuttings from a 7-year-old Sierra Nevada x coastal hybrid, collected in February, treated with indolebutyric acid (IBA), and rooted at 27° C, all produced roots in 4 months (Blankensop 1968). In Britain, five of six 9- and 10-year-old interprovenance hybrids (coast x interior, coast x coast) had 60 to 99 percent rooting success under optimal conditions, but the sixth had only 7 percent success (Bowen and others 1975). Trees 20 years old gave 87 percent rooting success (A. M. Fletcher, pers. commun., Jan. 1972), and 65 percent of the cuttings from upper branches of two 43-year-old trees rooted under optimal conditions (Bowen and others 1975). In a massive screening of rootability in Britain, about half the clones gave 60 percent or more rooted cuttings (Forestry Commission 1976).

The season of collection is apparently not too critical. Cuttings taken in Britain in March-April, July, and September have rooted successfully (A. M. Fletcher, pers. commun., Jan. 1972). Iktüeren (1973) obtained best results with cuttings from trees of coastal origin collected in January through July, depending on tree age and treatment. Bowen and others (1975) initiated successful rooting experiments in September, December, and February.

The most thorough investigation of factors affecting rooting was done in Britain, mostly with cuttings from interprovenance hybrids (Bowen and others 1975). In these tests, hormones dissolved in ethanol were applied to the freshly cut stem of cuttings 10 to 12 centimeters long, and rooting was in beds at 22° C under long photoperiods. Callus was often present at 3 to 4 weeks, and rooting was assessed at 3.5 to 4 months, when most roots had appeared. When the hormones IBA and NAA (naphthaleneacetic acid) were applied separately, IBA was effective only at the highest concentration (60 mg per cutting), and NAA was most effective at the lowest concentration (2 mg). In tests of other clones, mixtures of the two hormones (50:50 by weight) were most effective at an intermediate concentration, with reduced rooting at higher and lower concentrations. Boron, which is known to influence rooting, acted synergistically with high hormone concentrations to increase rooting sharply, but was ineffective alone. At lower hormone concentrations, the addition of boron depressed rooting. Clones differed strikingly in their response to IBA/NAA, with or without boron, and Bowen and others (1975) grouped them into four categories: (1) rooting poor and not affected by treatment, (2) rooting good and not affected by treatment, (3) rooting reduced by treatment, (4) rooting enhanced by low levels of hormone with or without boric acid, but depressed by high levels.

Hormones also influenced the type and number of roots. Untreated cuttings produced mostly micro-roots — much-branched roots of small diameter. IBA had little effect on root type, but NAA increased the production of large-diameter, mostly unbranched macro-roots, and at high concentrations greatly reduced the production of micro-roots. Bowen and others (1975) tentatively recommended treatment of lodgepole pine cuttings with 500 parts per million (p/m) NAA/IBA and 0.5 p/m boric acid.

Attempts to root needle fascicles have had limited success (Larsen and Dingle 1969). Fascicles were collected from trees of coastal origin 2 to 6 years old, and best results were obtained with December collection. Relatively few fascicles rooted, and only a small number of rooted fascicles produced shoots. More rooting was obtained with fascicles from 2-year-old trees, and the authors considered age an important factor. Iktüeren (1973) had significantly better rooting success with fascicles from 5-year-old trees compared with 3-year-olds, but fascicles from trees more than 5 years old rooted poorly.

Air-layering of 8-year-old interior lodgepole pines in Korea was highly successful, the best treatment giving 85 percent rooting in less than 2 months (Yim 1961). Mid-June treatment was significantly better than early July, and IAA (indoleacetic acid) gave better results than IBA, but untreated controls were not included. Despite the high percentage of rooting in the best combination, this method of propagation does not seem to have been used elsewhere.

Tissue Culture

Callus tissue cultures and liquid cell suspensions have been produced from seedling hypocotyl tissue, excised embryos, and actively growing shoots (Street and Webb 1975, 1976, 1977). Both kinds of cultures include living, dividing cells and dead tracheid-like cells with lignified walls. The proportion of the two cell types can be controlled by cultural conditions. These cultures have not produced organized structures, but the hypocotyl and cotyledonary regions of excised embryos can be induced to form meristematic nodules with high cytokinin:auxin ratios. These nodules have developed into leafy shoots that can be rooted by traditional techniques.

Variation in Natural Stands

Growth, Form, and Longevity

Regional variations in growth rate, maximum size, maximum age, and form are conspicuous but poorly documented. Trees in coastal stands grow fairly rapidly in youth (Critchfield 1957, appendix table 1), but seldom reach large sizes or great ages. On Vancouver Island and the adjacent mainland they may exceed 2 feet (61 cm) in diameter and 100 feet (30 m) in height (Roche 1963). The tallest tree Aldhous (1976) observed in the coastal muskeg type, on the west coast of Vancouver Island, was 32 meters. On the same type of site in the same region, most trees were about 15 feet (4.6 m) at 100 years (Pavlick 1971), but trees in a sphagnum bog in northwest Washington reached 55 feet (17 m) in 50 to 54 years (Kienholz 1931). In southeastern Alaska, Gorman (1896) noted an unusually large tree more than 100 feet (30 m) tall and 18 inches (46 cm) in diameter at the base. However, in the same region 120-year-old trees growing in a bog were only 13 feet (4 m) tall (Critchfield 1957). The oldest coastal tree on record (370 years) grew on northern Vancouver Island (Garman 1973). The largest coastal trees were on Graham Island, one of the Queen Charlotte Islands: 34 and 33.5 inches (86 and 85 cm) in diameter and 127 and 118 feet (39 and 36 m) in height (D. Pigott, pers. commun., Nov. 1978).

Mature trees on the Mendocino White Plains are smaller and possibly shorter-lived. The oldest trees so far reported were 87 to 92 years (Westman and Whittaker 1975). Tree height is highly variable on these extreme sites, and maximum height of older trees ranges from about 7 to 39 feet (2 to 12 m) (Critchfield 1957, Jenny and others 1969, Westman and Whittaker 1975).

Lodgepole pine reaches greater ages and larger dimensions in the Rocky Mountain-Intermountain region, but nowhere in this region is it a large tree, nor is it usually long-lived. Mason (1915) reported that Rocky Mountain stands more than 250 years old were uncommon, and stands older than 300 years were rare. The oldest stand mentioned by Mason, a 450-year-old stand in southwestern Montana, is still the oldest recorded for this region. Maximum stand ages in Alberta were in the same range, and the oldest was 375 years (Horton 1956). Lotan (1968) noted individual trees in eastern Idaho more than 400 years old, and unusually old trees of 315 and 346 years have been reported in northern British Columbia (Garman 1973) and Colorado (Mills 1915). In the southern Intermountain region lodgepole pine is apparently shorter-lived: maximum stand ages at low elevations in northern Idaho are 80 to 100 years (Lotan 1976), and the oldest tree noted in eastern Oregon was 173 years (Trappe and Harris 1958).

In interior British Columbia, lodgepole pine grows to heights of 130 feet (40 m) (Smithers 1961), and in the southern Washington Cascades to 138 feet (42 m) (Aldhous 1976)—the maximum reported for the species. The largest Rocky Mountain tree of record in 1915, a Colorado tree 34 inches (86 cm) in diameter and 100 feet (30 m) tall (Mason 1915), is still the largest. Elsewhere in the region, trees with unusually large diameters are in the range of 26 to 30 inches (66 to 76 cm): British Columbia, 30 inches (Smithers 1961); Alberta, 29 inches (Horton 1956); southern Montana, 26 inches (Mason 1915); and Colorado, 29 inches (Mills 1915).

In the California mountains, lodgepole pine reaches much larger diameters—and possibly greater ages—than elsewhere, but the trees are short in relation to their girth. The three successive largest lodgepole pines of record (American Forestry Association 1951, Pardo 1978) were all in the southern Sierra Nevada or the southern California mountains. The trees were 6 feet to 6 feet 9 inches (183 to 206 cm) in diameter and 91 to 110 feet (27.7 to 33.5 m) tall. Large-diameter trees are fairly common throughout the Sierra Nevada: of 313 0.2-acre (.08 ha) plots measured in the central and northern Sierra during the 1930's, 46 percent included trees 24 inches (61 cm) or more, and 8 percent had trees 36 inches (91 cm) or more. Many of these trees were only 50 to 100 feet (15 to 30 m) tall, but a few were up to 125 feet (38 m). Little information is available on the ages of these large trees, but one tree in the central Sierra Nevada near tree line had 321 annual rings in the outer third of its 55-cm radius, and its age was conservatively estimated as 600 years (Critchfield 1957, p. 17).

These and other scattered data suggest that the Sierra-Cascade race has a different pattern of height and diameter growth than the rest of the species. Initial height growth of central and south-central Oregon trees was slower than that of Rocky Mountain-Intermountain trees up to the age of about 50 (Alexander and others 1967, Dahms 1975). At 20 to 22 years planted Sierra Nevada trees were only 33 to 56 percent as tall as northern Rocky Mountain trees at several sites in Montana and Idaho (Rehfeldt and Lotan 1970). However, Sierra Nevada trees apparently have a more sustained rate of diameter growth. Trees in eastern Oregon (Trappe and Harris 1958) and in the southern Washington Cascades and a northwestern Washington bog (Kienholz 1931) all showed a rapid decrease in the width of annual rings up to an age of 30 to 60 years, stabilizing at widths of about 0.5 to 1.6 millimeters. Small samples of Rocky Mountain trees 10 to 20 inches (25 to 50 cm) in diameter had average ring widths in the same range: 0.47 to 1.43 mm (Bannan 1964). These trees were at elevations of 3,000 to 10,000 ft (900 to 3,050 m) in six localities from Alberta to Colorado. In contrast, trees of the same size at 8,000 feet (2,450 m) in the central Sierra Nevada had ring widths averaging 2.43 millimeters.

Coastal trees, especially in exposed situations, often have poorly formed and heavily branched crowns, in contrast to the narrower crowns and finer branches of trees in the Rocky Mountain-Intermountain region. In Alberta, trees in the subalpine forest typically have long, narrow crowns with fine, upswept branches, whereas in the boreal forest to the north and northeast the crowns are shorter and broader, with heavier, less upswept branches (Smithers 1961). Variations in crown form in natural stands were described and illustrated by Roche (1966) and Aldhous (1976).

Multinodal leaders are common. Data of R. W. Dingle on maximum number of branch whorls per spring shoot showed a range of 1 to 4 whorls on young trees in Washington and northern Idaho (Scobie 1971). Stand means were 1.7 to 2.4 whorls, with no obvious difference between coastal and interior localities.

Repeated stem forking is also common, unusually so in some central British Columbia stands (Aldhous 1976). Illingworth (1976b) noted a number of stands in which repeated forking appeared to be genetically controlled, and Franklin and Callaham (1970) found evidence of a partial genetic basis for this trait in progeny tests of multiple-forked trees growing in the Lake Tahoe region of California. In some California stands where multiple forking is prevalent, however, this deformity is caused by the lodgepole terminal weevil, *Pissodes terminalis* (Salman 1935, Stark and Wood 1964).

Near tree line in the southern Sierra Nevada, lodgepole pine occasionally grows as a shrub about 2 meters high. Clausen (1965) speculated that this elfinwood form, which is sometimes associated with lodgepole trees as large as 35 meters in height, is a distinct alpine ecotype or race.

Wood and Bark

The bark is highly variable, and differences in its character, color, and thickness have provided standard taxonomic distinctions between coastal and interior forms. Interior trees generally have thinner, scalier bark (fig. 2), and the freshly exposed surface is sometimes described as orange (Aldhous 1976), dull pink (Fosberg 1959), or yellow-orange (Lotan 1976). Stands in the southern Intermountain region do not always conform to this description: Lotan (1976) contrasted the black, deeply fissured bark of stands at low elevations in northern Idaho with the thinner, lighter-colored bark of high-elevation stands elsewhere in the northern Rocky Mountains, and Aldhous (1976) noted and illustrated (plate 10) stands with thick, fissured bark near Shuswap Lake in south-central British Columbia. In Alberta, the bark is considerably darker than in adjacent regions and more like that of jack pine (Smithers 1961). Variation in bark characteristics with site, age, growth rate, and region were described and illustrated by Roche (1966) and Aldhous (1976). Aldhous classified bark into four general types: platy (fig. 3), fissured-adherent (both coastal), scaly, and fissured-flaky (both interior).

A few observations suggest that wood properties are also extremely variable in natural stands. Sargent (1897) first compared coastal and interior wood. Coastal wood was denser (specific gravity 0.58, compared to 0.41), and had more summerwood and resin canals. Wells and Rue (1927) also noted that wood of Rocky Mountain trees had less pitch than that of coastal or lowland trees. A difference in amount of summerwood was confirmed by Kienholz (1931) in a small-scale comparison of wood from trees growing in a northwest Washington bog and in the Washington Cascades. In the age range of 10 to 50 years, the percent summerwood in the bog trees exceeded that of the montane trees by 32 to 100 percent.

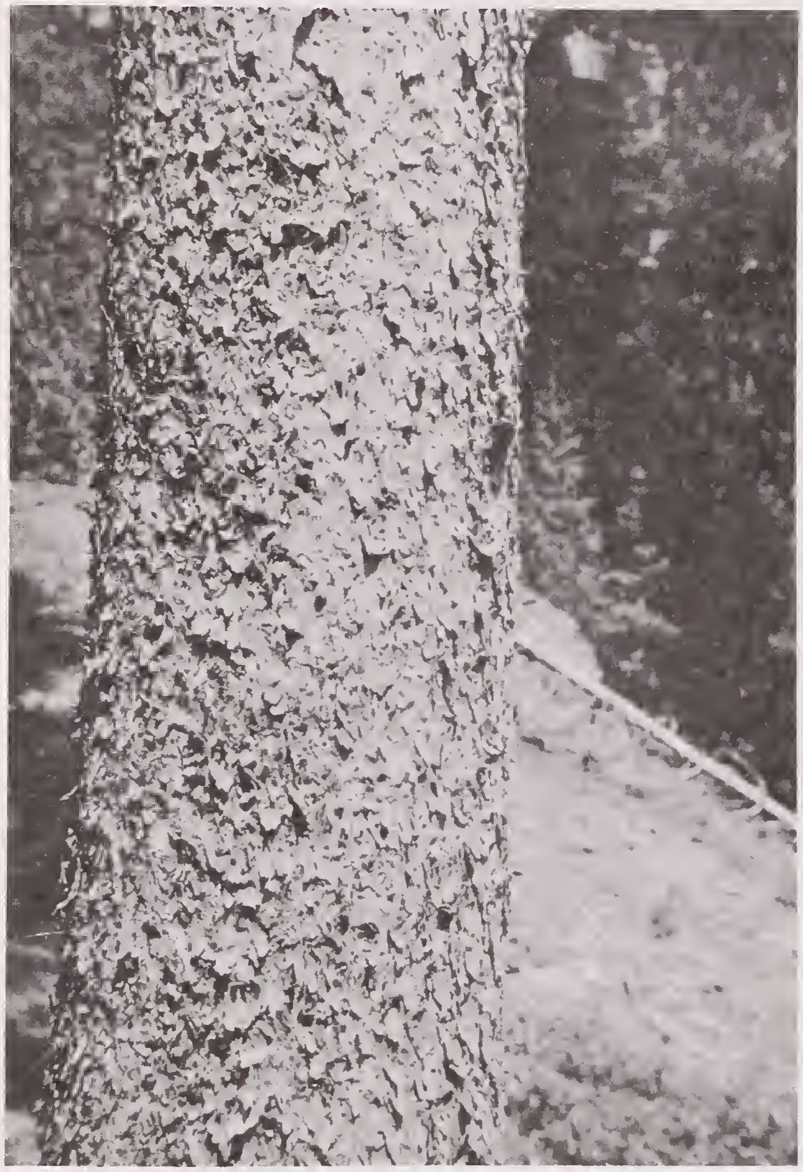

Figure 2.—Thin, scaly bark of a tree at Chinook Pass, Washington (from Roche 1966).

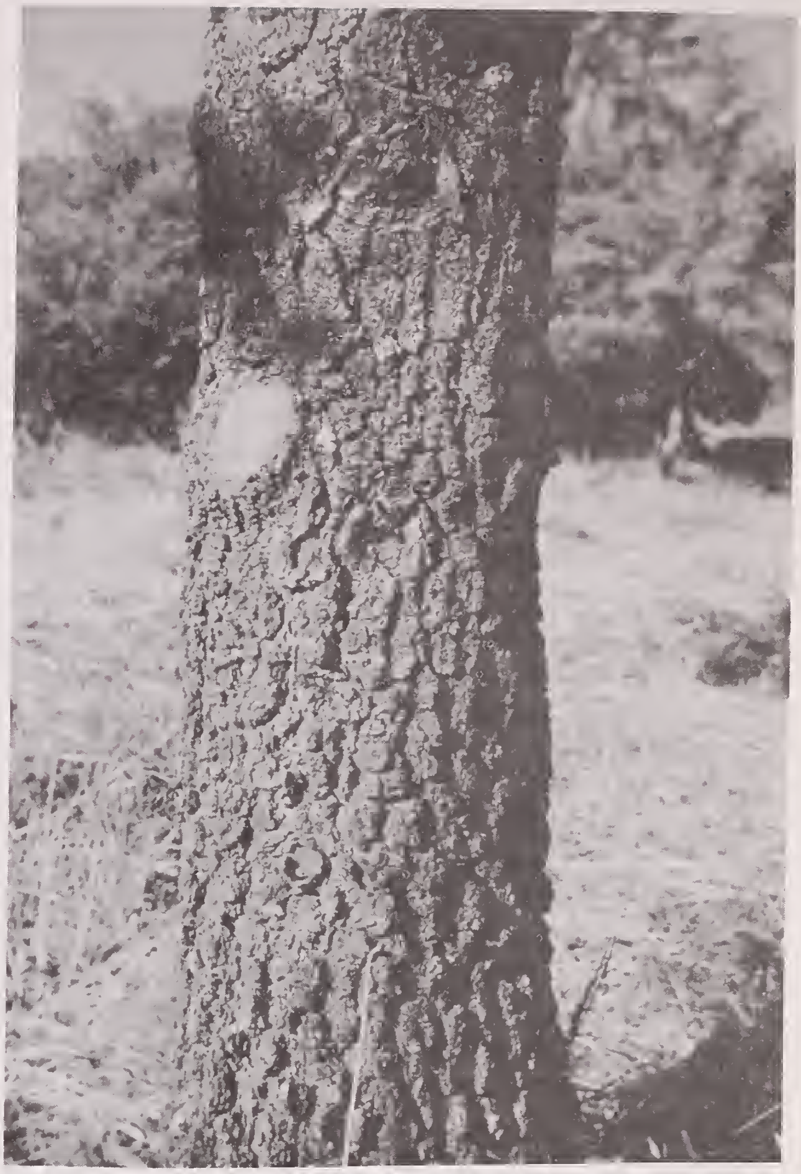

Figure 3.—Thick, platy bark of a tree near Olympia, Washington (from Roche 1966).

Leaves

Regional differences in leaf dimensions have often been exaggerated in classifications of lodgepole pine. The leaves of coastal trees are usually characterized as shorter and narrower than those of interior trees. For the entire species, Critchfield (1957) found a total range in leaf width of 1 to 2.5 millimeters, but most sample means were 1.4 to 1.7 millimeters. Mendocino White Plains trees and a sample from the coastal/interior transition in southwestern British Columbia had narrower leaves (1.3 mm). Stands on southern Vancouver Island and the Queen Charlotte Islands also had leaves averaging 1.3 millimeters wide (Illingworth 1971). Southern Cascades and Sierra

Nevada trees had the widest leaves, with most sample means 1.6 to 2.0 millimeters (Critchfield 1957). Width increased with elevation in this region and in interior British Columbia, where a high-elevation sample had much wider leaves (1.6 mm) than a nearby low-elevation sample (1.2 mm) (Illingworth 1971).

Leaf length has received less attention, but most coastal samples have shorter leaves than most low- and mid-elevation interior samples (Critchfield 1957). This difference was pronounced in British Columbia, where two coastal stands sampled by Illingworth (1971) had much shorter leaves (means 35 and 39 mm) than three interior stands (means 48 to 57 mm). Among Critchfield's (1957) samples, Mendocino White Plains and high-elevation Sierra Nevada trees had the shortest leaves (31 to 46 mm). In the Sierra, leaf length decreased with increasing elevation.

On older trees, fascicles with more than two leaves have been reported only in the northern part of the range, although they are occasionally present on 1st-year seedlings (Sweet and Wareing 1968). Fascicles with three or more needles have been noted in the Atlin region just south of the Yukon border (Garman 1973) and are common at high elevations in the central and south-central Yukon, on the margins of the unglaciated part of the Yukon (von Rudloff and Nyland, 1979), and in a timberline stand near Jasper, Alberta (Pollack and Dancik, 1979). A stand near Mayo, Yukon, with many three-needled fascicles was described as a new variety of *P. contorta* in an unpublished report[2].

The concentration of stomata on the flat (adaxial) face of the leaf was investigated by Illingworth (1975) in British Columbia. Two widely separated coastal stands were nearly identical (63 to 64 per mm^2), and both were significantly higher in stomatal number than three interior stands (40 to 59 per mm^2). A low-elevation interior stand had more stomata than a nearby high-elevation stand or a distant high-latitude stand.

Stomatal shape also varies regionally (Critchfield 1957). Leaves of coastal trees and, to a lesser extent, Rocky Mountain-Intermountain trees, have a well-defined, partly enclosed epistomatal cavity formed by flange-like extensions of the subsidiary cells. In the leaves of Sierra Nevada trees these extensions are not well developed, and the cavity has a wider external opening (Critchfield 1957, fig. 11).

The resin canals at the midpoint of the leaf number 0 to 7, but most leaves have 0, 1, or 2 (Critchfield 1957). Throughout much of the species range, most trees average 1 to 2 canals per leaf, but in a few places resin canals are scarce or absent. The leaves of the isolated population on the Mendocino White Plains and adjacent coast had no resin canals, and few were present in other southern coastal samples and scattered interior localities. North-coast populations averaged 1.9 to 2.0 canals per leaf (Critchfield 1957, Illingworth 1971). In the Sierra Nevada, the number of resin canals increased with elevation, paralleling the increase in leaf width, and averaged 1.9 to 2.0 canals per leaf in high-elevation populations (Critchfield 1957).

Reproductive Structures

Variations in natural stands in reproductive phenology, cone serotiny, seed weight, cotyledon number, and germination behavior were described elsewhere (see *"Sexual Reproduction"*). Several other cone characteristics roughly parallel the regional variation in serotiny. Cone specific gravity or density and the features associated with it (cone hardness, apophysis form) are among the most variable and geographically differentiated characteristics of lodgepole pine. In Critchfield's (1957) sampling, cones of individual trees averaged 0.43 to 0.89 in specific gravity, and stand means were 0.50 to 0.79. Specific gravity was generally highest in the Rocky Mountain and northern Intermountain regions, decreasing in the southern Intermountain and northern Cascade regions, and lowest in the southern Cascades and Sierra Nevada. Coastal stands were intermediate and rather uniform, but closed-cone populations near the coast had heavier cones. Mendocino White Plains trees had denser cones than trees on the nearby coastal bluffs, and cones of the Del Norte race had the highest specific gravity encountered (0.86), compared with 0.62 for cones from the coast 15 miles (24 km) to the west.

---

[2] Krajina, V. J., and O. Sziklai. 1976. Environmental study of a relict race of lodgepole pine in central Yukon. Univ. British Columbia, Vancouver.

Variations in cone hardness and apophysis form follow the same geographic pattern. The hard, heavy cones of Rocky Mountain trees have protruberant basal apophyses, often pyramidal, conical, or mammiform in shape. At the other extreme, the relatively light-weight, soft, fragile cones of Sierra Nevada trees have relatively flat apophyses. Coastal and geographically intermediate interior stands are generally intermediate in apophysis form and cone hardness. Variations in apophysis form were illustrated by Critchfield (1957).

Outside the Sierra-Cascade region, the cones have a well-developed woody cylinder in the pedicel, and in most stands they remain on the tree indefinitely (Critchfield 1957). In the pedicels of Sierra-Cascade cones the woody cylinder is small in diameter. The cones often fall off the tree soon after they mature, and are nearly always shed within a few years.

The orientation of the cone on the branch provides much of the evidence that jack pine may have influenced lodgepole pine in regions remote from the areas where they now grow together. Lodgepole cones are mostly reflexed, but the angle formed by the relatively straight cone axis and the terminal part of the cone-bearing branch shows a total range of about 45° to 155° (Critchfield 1957). Jack pine cones may be straight or curved (Schoenike 1962). They are not reflexed except in and near the overlap region. Occasionally they are perpendicular to the branch and in a few instances have cone angles of 95° to 100°, but most commonly they are incurved or semi-erect (attached at an acute angle). If curvature is very marked, negative angles up to 45° may be formed by the branch and a line through the tip and base of the cone (Schoenike 1962, Schoenike and others 1959).

In Critchfield's (1957) survey of lodgepole pine, cones from coastal stands were uniformly reflexed, with sample means of 124° to 137°. This orientation was even more pronounced in closed-cone stands near the coast: cones of the Del Norte race had the largest angles (mean 146°) encountered in lodgepole pine. In the Sierra-Cascade region, most cones were perpendicular or slightly reflexed, with sample means of 89° to 108°. At upper elevations, some trees had cones attached at angles of 70° to 90°.

Cone orientation was more variable between stands in the Rocky Mountain-Intermountain region, with sample means of 81° to 123°. Within-stand variation was highest in the northern Rocky Mountains, where trees with semi-erect cones like those of jack pine were present in the same stand as trees with typical reflexed cones. The range of tree means in the region was 45° to 130°. Northern Rocky Mountain samples had significantly larger coefficients of variation (30 to 35) than coastal or Sierra-southern Cascade samples (6 to 15) (Critchfield 1957).

Cone orientation in the interior of western Canada was intensively sampled by Illingworth (pers. commun., Jan. 1973). The incidence of trees with semi-erect cones increased from 0 in the Yukon to 5 percent in the north half of British Columbia (north of latitude 54°30′) and 14 percent in the south half of the Province. Stands in the Peace River region of northeast British Columbia, nearest the zone of current hybridization, had about the same frequency of semi-erect cones as other stands in northern British Columbia. The highest frequencies of semi-erect cones (25 to 50 percent) were in several stands scattered through south-central and southeastern British Columbia. This cone type was also present in southwestern Alberta but absent in an Alberta sample closer to the western limits of jack pine.

Limited data from the southern Rocky Mountains indicates that trees with small cone angles are occasional or rare there (Critchfield 1957, and personal observations). Semi-erect cones have not been noted south of the Canadian border in the Cascades or the southern Intermountain region.

The seed of lodgepole pine is variable in shape as well as size. In a comparison of coastal and interior seeds, the former were slightly shorter, less prominently ridged, and less pointed at the end opposite the micropyle (Roche 1962, fig. 6).

Sierra Nevada pollen averages larger than that of the rest of the species, and may differ in morphological detail. Axelrod and Ting (1960) compared pollen of the Sierra Nevada race with coastal pollen. Body length was larger (54 to 58 μ compared with 38.5 to 52 μ), and the reticulations on the pollen wings were very coarse and distinct compared with the fine reticulation of coastal pollen. Mack (1971) found nearly complete overlap in body size of pollen from natural stands of the coastal and Rocky Mountain-Intermountain regions. In his two samples of Sierra pollen the body size was 51 and 56 μ compared with a range of 41 to 53 μ in a much larger number of coastal samples.

Resin

In the Sierra-Cascade and coastal regions, the principal monoterpene (> 50 percent) of the wood resin is β-phellandrene, with lesser amounts of α- and β-pinene and 3-carene (Mirov 1961; Smith 1964, 1967). In the northern Rocky Mountains, resin composition shifts in the direction of jack pine, in which the monoterpene fraction consists almost entirely of the two pinenes (Zavarin and others 1969). In eastern Idaho and northern Montana samples, the mean percentage of β-phellandrene was lower and that of the pinenes was higher than in Oregon and California (R. H. Smith, pers. commun., June 1977). A few trees in Montana, southern Alberta, and southeastern British Columbia had more α-pinene, β-pinene, or 3-carene than β-phellandrene (Lotan and Joye 1970, Shrimpton 1972). In lodgepole stands 37 to 50 miles (60 to 80 km) from the limits of jack pine in Alberta, about half of the trees had only 18 to 40 percent β-phellandrene (Mirov 1956)—close to the levels in F_1 hybrids between lodgepole and jack pines (Zavarin and others 1969).

Stem cortex resin is similar in composition to xylem resin, with β-phellandrene and α-pinene the principal monoterpenes in lodgepole and jack pines, respectively (Dancik 1979). In an analysis of the two species throughout Alberta, J. C. Pollack found variant monoterpene types in all lodgepole stands sampled in the Rocky Mountains, extending south almost to the American border, but no variants in his lodgepole sample from the isolated Cypress Hills, on the Alberta-Saskatchewan border (Dancik 1979). Pollack interpreted these variants as evidence of introgression from jack pine into lodgepole pine.

The composition of leaf resin has also been investigated in western Canada, with results that are more difficult to interpret. In and near Alberta, most lodgepole pines sampled by Pauly and von Rudloff (1971) differed from a bulk sample of Saskatchewan jack pine resin in about a dozen identifiable constituents, including the four principal monoterpenes of wood resin. They found no trees with intermediate resin in the Cypress Hills, and few in the Banff region and nearby foothills. From Banff north to the western limits of jack pine, however, 10 to 15 percent of the trees they sampled were intermediate in several compounds, and two intermediates also resembled jack pine in lacking cone prickles. Their interpretation—that jack pine had influenced lodgepole pine through introgression—was later reconsidered when jack pines with similar intermediate composition were found in eastern Canada (von Rudloff 1975).

A few intermediate trees—low in β-phellandrene and high in both pinenes—were also found in glaciated and unglaciated parts of the Yukon (von Rudloff and Nyland 1979). They were greatly outnumbered by the common interior type, which is higher in β-phellandrene and lower in α-pinene. Intermediate trees were more frequent in the Liard Range of southwestern Mackenzie District: 4 intermediates of 10 trees sampled, compared with 3 of 79 in the Yukon. The Liard Range is near Nahanni Butte, where lodgepole and jack pines meet and hybridize. (See *"Natural hybridization and introgression."*) A third resin type, high in β-phellandrene and low in both pinenes, characterized about one-third of the trees in the Yukon and Liard Range and all trees in two coastal samples (Vancouver Island and Oregon). Von Rudloff and Nyland speculated that the diversity of resin composition in northern populations might be related to the existence of Pleistocene refugia in the unglaciated Yukon.

A remarkable feature of these data on leaf resin composition is the tendency for groups of monoterpenes to vary together. This behavior is in contrast to the independence of individual monoterpenes in wood resin (Zavarin and others 1969).

Pests

Some parasites and predators of lodgepole pine exhibit geographic differences or restricted distributions that may reflect inherent differences between host populations or races. One example was described elsewhere (see *"Sexual Reproduction"*): the replacement of red squirrel by Douglas squirrel in the region where the closed-cone Rocky Mountain-Intermountain race grades into the open-cone coastal and Sierra-Cascade races. The distributional or variation patterns of several diseases and insects also suggest host-race specificity.

Three dwarf mistletoes have limited distributions on lodgepole pine. The two interior races of lodgepole pine and western populations of jack pine are about equally susceptible to the lodgepole pine dwarf mistletoe *(Arceuthobium americanum)* (Hawksworth 1975). This destructive mistletoe infects a large proportion of interior lodgepole stands. It occurs on shore pine only in one locality, north of Vancouver, British Columbia, where it extends within 8 miles (13 km) of the coast (Baranyay 1975). This coastward extension was unknown when Kuijt (1963) concluded that the western limits of the mistletoe could probably not be attributed to differences in host-race susceptibility. Its presence near Vancouver indicates that it is not climatically excluded from the coastal region, and differential susceptibility now seems a more probable explanation for its absence from shore pine generally.

Another member of this group, hemlock dwarf mistletoe *(A. tsugense)*, occurs on shore pine in British Columbia and northwest Washington, and is common in some stands on Vancouver Island (Wass 1976). Its primary host is western hemlock, but shore pine is often heavily infected in places where hemlock is either absent or not infected. This observation and cross-inoculation tests (Smith 1974) suggest that the mistletoe on shore pine is a different ecological race from that on hemlock. Hemlock dwarf mistletoe has never been reported on lodgepole pine outside this region (Hawksworth and Wiens 1972), although the mistletoe ranges as far south as the central Sierra Nevada on mountain hemlock, a high-elevation associate of lodgepole pine.

One of the primary hosts of the digger pine dwarf mistletoe *(A. occidentale)* is bishop pine *(P. muricata)*, which grows with lodgepole pine on the Mendocino White Plains and the nearby coast. Bishop pine is infected in both areas, but the mistletoe has been reported only on the White Plains race of lodgepole pine (Hawksworth and Wiens 1972).

The mountain pine beetle *(Dendroctonus ponderosae)* is the most destructive insect pest of lodgepole pine, causing heavy mortality in stands of the interior West. In an analysis of genes controlling enzymes (isozymes), Stock and others (1978) found that beetles from a locality in south-central Oregon differed appreciably from beetles collected in three localities in northern Idaho.

Several taxa in the insect genus *Coleotechnites (= Recurvaria, Evagora)* mine lodgepole pine needles. The best known is *C. milleri*, which defoliates and frequently kills trees in and near the Yosemite region of the Sierra Nevada (Koerber and Struble 1971). A needle miner of undetermined status, differing from *C. milleri* in habits and life cycle (T. Koerber, pers. commun., July 1977), occurs in lodgepole stands on the east side of the Sierra Nevada. Another needle miner, differing from both California forms, partially defoliated extensive tracts of lodgepole pine in central Oregon but caused little or no mortality (Mason and Tigner 1972). Two other needle miners occur in the Canadian Rockies: *C. starki*, which has periodically caused extensive defoliation of subalpine lodgepole pine in Alberta and British Columbia (Stark 1954), and *C. canusella*, reported on lodgepole pine near Shuswap Lake, British Columbia (Koerber and Struble 1971) and on jack pine in eastern Canada (McLeod 1961).

Another insect, the lodgepole terminal weevil *(Pissodes terminalis)*, kills the leaders of young lodgepole and jack pines, and is believed to be responsible for the deformities so common in some California stands (Salman 1935, Stark and Wood 1964). This weevil occurs on jack pine in Saskatchewan and Manitoba (Drouin and others 1963) and has been reported at widely separated places through most of the inland range of lodgepole pine (Drouin and others 1963, Stark and Wood 1964, Amman 1975). Typical *Pissodes* damage has also been observed in Mendocino White Plains stands (Stark and Wood 1964). The weevil is chromosomally polymorphic and thought to be of hybrid origin (Drouin and others 1963). The race that infests lodgepole and jack pines in western Canada is grossly different in morphology and biology from the strain in the Sierra Nevada and southern Cascades (Drouin and others 1963, Stark and Wood 1964), but the affinities of the weevil in other regions are unknown.

Two minor insect pests have been reported on single races of lodgepole pine. The lodgepole bark beetle *(Dendroctonus murrayanae)*, which occasionally kills old trees left after logging (Keen 1952), is restricted to jack pine and the Rocky Mountain-Intermountain race of lodgepole pine (Wood 1963). *Paritimia conicola*, the only North American longhorn beetle known to feed regularly on cones, attacks two closed-cone California pines, *P. attenuata* and the White Plains race of *P. contorta* (Linsley 1962).

Natural Hybridization and Introgression

Pinus contorta and *P. banksiana* hybridize in both regions where they overlap: central and west-central Alberta between Edmonton and the Peace River-Grand Prairie region, and the southwest corner of the Northwest Territories near Nahanni Butte. Hybridization in the Nahanni Butte region was reported by Cody (1963) and Scotter (1974). Cody also found putative hybrids at two locations north and east of the known range of lodgepole pine. Scotter's collections of lodgepole pine west of the Nahanni Butte area show little or no influence of jack pine.

Hybridization has been more thoroughly investigated in the broader region of overlap in Alberta. Hybrids were first noticed by A. C. Holman (Austin 1929) and E. H. Moss (Raup 1942). Moss later surveyed the frequency and extent of hybridization, using such criteria as cone orientation, curvature, and presence or absence of cone prickles (Moss 1949). He found hybrids in many localities within the overlap zone, together with one or both parent species. Only in a few places did intermediates outnumber the parent species. Mirov (1956), utilizing chemical and physical properties of turpentine, confirmed Moss's observation that hybridization is common in the overlap region.

Outside the overlap zones, lodgepole pine has influenced some western and northern populations of jack pine, but the degree of influence appears to bear little relation to distance from the nearest lodgepole stands. Jack pine at Bruderheim, Alberta, only about 50 miles (80 km) east of the principal overlap zone, shows little or no lodgepole influence in its morphological (Moss 1949, Schoenike 1962) or chemical (Mirov 1956) characteristics. But lodgepole-like characters are present in jack pine stands 220 to 500 miles (350 to 800 km) east of the nearest known outliers of lodgepole pine, including Schoenike's (1962) samples from Glaslyn and Cree Lake in western and north-central Saskatchewan and stands in the extreme northeast corner of Saskatchewan (Argus 1966). The available evidence is insufficient to discriminate between several possible explanations of this distribution: (1) contacts between the species during the Pleistocene, (2) post-Pleistocene introgression (the spread of genes away from the area of hybridization, as defined by Heiser 1959), or (3) local foci of hybridization resulting from pollen transported for long distances by prevailing westerly winds.

Evidence that jack pine has influenced lodgepole pine far beyond the regions where they overlap, as proposed by Critchfield (1957), was reviewed by Zavarin and others (1969). Although it is limited and somewhat contradictory, this evidence suggests that in lodgepole pine, as in jack pine, the degree of influence bears little relation to distance from the nearest populations of the other species. Moss (1949) found little or no jack pine influence in those parts of Alberta and British Columbia immediately south and west of the principal overlap zone. More extensive data on cone orientation—probably the most reliable morphological indicator of jack pine influence because of the virtual absence of semi-erect cones outside the northern Rocky Mountain region—is generally in agreement. Semi-erect cones are most common in regions remote from the overlap zone—southern Alberta, southeastern and parts of central British Columbia, and Montana—not adjacent to this zone. The data on wood and cortex resin composition are too limited to indicate degree of jack pine influence, but they do support the view that this influence extends beyond west-central Alberta. In lodgepole pine, in contrast to the situation in jack pine, topographic barriers and prevailing wind direction make it improbable that long-distance pollen transport could be responsible for localized jack pine influence in places remote from the overlap region. A more likely explanation is that (1) post-Pleistocene influence of jack pine is mostly restricted to the regions of overlap, and (2) outside these regions, widespread but nonuniform jack pine influence is the result of earlier contacts between the species, perhaps during Pleistocene interglacials in which their distributions approximated their contemporary distributions.

A different view was expressed by Yeatman (1967), who argued that the two pines came together for the first time a few thousand years ago. He based his argument principally on two kinds of evidence: (1) the limited and apparently immature stage of introgression in and near the Alberta overlap zone, and (2) the late-Quaternary migrational history of jack pine. He accepted Wright's (1964) conclusion, based largely on palynological evidence, that after Wisconsin glaciation jack pine reoccupied the Great Lakes region from a refugium in the Eastern United States. Extending these arguments to western Canada, Yeatman concluded that jack pine occupied its entire present range from an eastern refugium, reaching western Canada late in postglacial time.

More recent pollen evidence tends to support Löve's (1959) view that jack pine also had a western refugium, from which it occupied its range in western Canada. Pine appeared at a cluster of sites in northern Saskatchewan and Manitoba 6,500 to 6,000 years ago, later migrating south to several sites near the southern edge of jack pine's present range (Mott 1973, Ritchie 1976). Jack pine is the only pine in this part of Canada, but the identity of the pine that appeared at two sites in east-central Alberta about 7,500 years ago (Lichti-Federovich 1970, 1972) is less certain. These Alberta sites are within the range of jack pine and are about 20 to 60 miles (30 to 100 km) east of the present more or less continuous distribution of lodgepole pine. Ritchie (1976) interpreted the sequence of radiocarbon dates from Alberta to Manitoba as evidence for the eastward migration of jack pine from a refugium somewhere east of the Rocky Mountains. But the existence of lodgepole pine outliers in northeastern Alberta, including the Caribou and Birch Mountains (Critchfield and Little 1966) and the Christina Highland (Achuff and LaRoi 1977) indicates that lodgepole pine may have had a more extensive range to the east and northeast at some time during the postglacial period.

The evidence that jack pine may have had a western refugium raises the possibility that it and lodgepole pine were in sporadic contact during glacial as well as interglacial periods. This western refugium could have been in the hypothetical ice-free corridor east of the Rocky Mountains, or it could have been located on the unglaciated highlands east of the Rockies and near the southern edge of the ice. Among the latter possibilities are the Cypress Hills of Saskatchewan and Alberta (Newsome and Dix 1968) and several isolated ranges in north-central Montana (Lemke and others 1965) now occupied by poorly known outliers of lodgepole pine.

Variation in Provenance Tests

The first plantations from seed of known origin were established in northwestern Europe in 1902 to 1916. Encouraging early results in Finland (Tigerstedt 1922, 1927) and Ireland (Forbes 1928) stimulated fairly widespread planting in the late 1920's and early 1930's, mostly with seed of unknown origin. In the British Isles and New Zealand, a distinction emerged between faster-growing "green" coastal strains and slower-growing "yellow" interior strains. Known provenances sampled only a small part of the species range: part of the southern interior of British Columbia, Alberta, and a few poorly identified localities in the United States. The first large tests, including 30 geographic origins, were established at several places in Britain in 1937 to 1942 (Lines 1976b). The results of these and other early tests were summarized by Edwards (1954, 1955).

Two general conclusions could be drawn from these early tests: (1) lodgepole pine probably had greater variation associated with provenance than any other forest tree commonly planted in Europe (Lines 1966), and (2) interactions between provenance and country (or region) were large. Most coastal sources did not survive in the cold continental climates of Finland and Sweden, and in these countries interest has since been restricted mostly to central and northern interior sources. In the mild climates of Ireland and New Zealand, the superiority of coastal provenances was so marked that interior provenances were largely excluded from further consideration. In colder maritime climates like that of northern Britain, no single race showed comparable superiority, and large provenance × site interactions were common.

After World War II, lodgepole pine was planted on a much larger scale in several European countries. Of total trees planted, it made up 31 percent in Ireland by 1954 to 1957 (Mooney (1957), 18 to 19 percent in Britain by 1972 (Lines 1976c), and almost 10 percent in Sweden by 1975 (Lindgren and others 1976). In Ireland and Britain, it is used chiefly for the afforestation of peatland and other sites too poor for other tree species. In northern Sweden, where tests begun in 1930 to 1950 showed that it often grew faster and produced more volume than the native *P. sylvestris*, it is competitive for the better sites. Accompanying this expanded use were more ambitious provenance tests in several European countries and New Zealand, mostly established in the 1960's. These efforts of individual countries were supplemented in the late 1960's by the IUFRO seed collections—the most extensive and carefully documented set of lodgepole pine provenances ever assembled. Information on the early performance of IUFRO and other recent tests was summarized by Lines and others (in Lines 1976b).

Survival and Hardiness

Most lodgepole pine provenances are cold-hardy in relatively mild climates. All provenances were frost-hardy even on relatively cold sites at 2,200 to 3,100 feet (670 to 950 m) in New Zealand (Miller 1969), although in one test above timberline at 4,800 feet (1,460 m), survival of a naturalized strain of coastal origin and a provenance of the Del Norte race was lower than that of interior sources (Cunningham and Roberts 1970).

In colder maritime climates, low-elevation provenances from southern latitudes may be badly damaged by cold. In northern Scotland, southern Oregon and California coastal provenances do not fully harden in the autumn and are damaged or eliminated by winter cold (R. Lines, pers. commun., June 1978). Severe damage to Oregon-coast sources in Denmark during an unusually cold winter led Løfting (1966) to conclude that the Columbia River was the approximate southern limit for coastal provenances suited to Danish conditions. One of several experiments in southern Norway suffered winter injury to the needles after 3 years in the field (Robak 1976). Among six Alaska and interior British Columbia provenances, the most northern Alaska source (Skagway) had significantly less damage than the others, and the southermost interior source (52° latitude) had significantly more. In a plantation on the coast of northern British Columbia, seedlings of north-coastal origins showed a pronounced gradient of increasing cold resistance between the outer and inner coast; sources from farther south were damaged more severely and uniformly (Illingworth 1976c).

In cold continental regions, provenances from low latitudes, low elevations, or maritime climates suffer heavy mortality. A severe winter at a central British Columbia nursery killed or badly damaged many seedlings of coastal origin, the extent of damage showing a clinal pattern (Illingworth 1975). Coastal Oregon and California provenances suffered 66 to 100 percent damage; and coastal Washington and Vancouver Island provenances suffered 3 to 36 percent, with a sharp break at the Columbia River. In freezing experiments with seedlings from single Vancouver Island and northeastern British Columbia sources at the end of their second growing season in northern Sweden, coastal seedlings were slower to develop frost resistance, and achieved a lower level than interior seedlings (Hagner 1970). In Swedish field tests, marked differences in survival at 9 years were related to latitude of seed source. Most of the provenances in these plantations—the first to sample the extreme northern interior—were concentrated in interior British Columbia and the Yukon. At lower-elevation sites in central Sweden, all provenances survived well after 5 years in the field; but on colder sites, survival showed a latitudinal gradient, with heavier losses in southern sources. At the coldest sites, near the Arctic Circle, this gradient steepened, and the more southern provenances survived poorly or not at all. At all sites, the best provenances equalled or exceeded native *P. silvestris* in survival (Hagner 1970).

Greater differences in mortality were observed at 6 years among a more diverse set of IUFRO provenances after 4 field seasons at 13 sites in central and northern Sweden (Lindgren and others 1976). In 31 of 37 provenances north of 54°01′ latitude, including six of seven Alaska sources, average mortality on all sites was less than 20 percent. Northern sources with higher mortality included one from the outer Alaska coast and several from the coast-interior transition in western British Columbia (Skeena River region). Among provenances south of 54°01′, 43 of 46 averaged more than 20 percent mortality. All 23 samples from the conterminous United States were in this group, and the two southernmost coastal samples (Puget Sound region) had the highest mortality: 75 and 71 percent. At two sites north of the Arctic Circle, the only provenances averaging less than 30 percent mortality were from the Yukon, extreme northern British Columbia (north of 58°), and a few places in coastal Alaska. Elevation of seed source had little influence on mortality of provenances north of 49°, but among the American provenances mortality decreased with increasing elevation.

Physiological characteristics of seedlings have been used in Scandinavia to measure cold-hardiness indirectly. In a southern Norway nursery study of provenances from the southern two-thirds of the species range, Dietrichson (1970) looked at dry-matter content of needles, anthocyanin pigmentation, and lignification of the outermost annual ring at the end of the growing season. Needles of 2-year-old seedlings in early winter ranged in dry-matter content from 22 percent (coastal California) to 29 percent (Alberta, Montana, and Wyoming). As latitude, elevation, and distance from the coast increased, anthocyanins and dry-matter content increased, annual rings lignified earlier, and post-storage mortality decreased. Sierra-Cascade provenances, however, produced much less anthocyanin than Rocky Mountain provenances of comparable latitude and elevation.

Autumn color showed the same trends in a test covering most of the species range (Illingworth 1975). At the end of one season in a Vancouver Island nursery, 12 to 13 percent of Alaska seedlings had developed autumn color (due to anthocyanin production) by mid-September, compared to 4 or 5 percent for coastal provenances south of Alaska. Among interior provenances, Sierra-southern Cascade provenances had the fewest seedlings (6 percent) with autumn color, and the northern Cascade region was transitional (17 percent). Other interior regions ranged from a high of 66 percent in the Yukon and northern British Columbia, to a low of 21 to 25 percent in a cluster of provenances in southeastern British Columbia. Illingworth observed a close relationship of autumn color with latitude, but not with elevation. He also noted qualitative differences: Sierra Nevada provenances turned a distinctive lilac, and those from the northern interior ranged from bronze-red to dark purple-gray. Similar color differences between coastal, northern, and Sierra-Cascade seedlings were noted in a large-scale test in Scotland (Forestry Commission 1970).

The early estimation of cold hardiness was also investigated by Hagner (1970) in 2-year seedlings of northern provenances grown in Sweden. In British Columbia samples, lignification was most closely related to latitude and to temperature-based climatic variables, followed by dry-matter content and a measure of earliness of shoot elongation. Dry-matter content (24 to 33 percent) was generally consistent with the values of Dietrichson (1970). Earliness of terminal-bud formation was the only character significantly correlated with elevation and unrelated to latitude. Local differentiation was suggested by the unexpected behavior of two Yukon provenances, the most northern and western samples in the study. In their low degree of lignification and lateness of terminal-bud formation, they resembled samples from 350 to 700 miles (550 to 1,100 km) farther south. These Yukon provenances nevertheless showed high survival at 9 years in the extreme north of Sweden (Hagner and Fahlroth 1974), illustrating the limitations of early, indirect measures of cold hardiness.

Provenance differences in dry-matter content of needles persist beyond the seedling stage, but the percentage of dry matter increases. It ranged from 31 (coastal California) to 38 percent (Alberta) in a 6-year-old plantation of 45 provenances in Scotland, with highly significant differences between groups of provenances (Forestry Commission 1976; R. Lines, pers. commun., June 1978).

Lodgepole pine provenances showed marked differences in wind-blasting damage (foliage browning and bud kill) on a site in northeast Scotland (Forestry Commission 1967). At 3 years, provenances from the outer coast of Washington and Oregon were least damaged, with scores of 41 to 46. Provenances from less exposed parts of the coastal region (Puget Sound, southern Vancouver Island) and from interior regions were more badly damaged, with scores of 55 to 71 and 57 to 64.

In a small-scale test of drought resistance, 2-year-old potted seedlings of a Sierra Nevada provenance (Yosemite) were much less susceptible to moisture stress than seedlings of five provenances from coastal Alaska and a wide range of latitudes and elevations in interior British Columbia (Dykstra 1974). The Yosemite seedlings had higher survival under extreme drought, and continued to grow at moisture levels too low for growth of the other provenances. The five northern provenances, although they varied significantly among themselves, formed a relatively homogeneous group compared with the Yosemite source.

Growth, Yield, and Form

In the mild climate of New Zealand, all but the northernmost coastal provenances are superior to most interior provenances in height and volume growth. In one test on a range of sites, all coastal sources (Puget Sound to California) exceeded all interior sources in height at 5 to 6 years, and were 3 to 4 times as tall as the slow-growing provenances from the California mountains (Miller 1969,[3]). In another 6-year-old test, consisting mostly of IUFRO-collected coastal provenances from Vancouver Island to the California coast, the southernmost sources and several local provenances of coastal origin produced 4 to 5 times as much volume as the northernmost[4]. In favorable circumstances, New Zealand "green" strains sustain much higher rates of diameter growth than trees in their native habitat (Harris 1971), and on better sites may produce as much as 700 cubic meters per hectare at 35 to 40 years (Miller 1969). Even on a harsh timberline site, local "green" strains were growing faster than interior provenances at age 10 to 11 (Cunningham and Roberts 1970).

Other tests in mild climates at lower latitudes show a similar pattern. In a small plantation at Placerville, California, all coastal (Vancouver Island to California) and Mendocino White Plains provenances were taller at age 7 than any interior source (central British Columbia to Colorado and the southern Sierra Nevada) (Roche 1962). In a Vancouver Island nursery test covering much of the species range, central- and south-coastal provenances were tallest at 2 years (Illingworth 1975). Alaskan and most interior provenances were much shorter, but a cluster of provenances in southeastern British Columbia and the adjacent United States was similar in height to coastal provenances at the same latitude.

---

[3] Miller, J. T. 1971. Provenance variation in growth rate and other characters in 6-year-old *Pinus contorta* in New Zealand. N.Z. For. Res. Inst. Genet. and Tree Improv. Rep. 55.

[4] Shelbourne, C. J. A., and J. T. Miller. 1976. Provenance variation in *Pinus contorta*—6 years results from IUFRO seedlots in New Zealand. N.Z. For. Res. Inst. Genet. and Tree Improv. Intern. Rep. 102.

In the colder climate and higher latitude of northern Britain, the superiority of coastal provenances is not as pronounced or consistent. In one of the oldest tests for which volume data are available, an unreplicated test planted in 1938 and 1939 in northeastern Scotland, a northern Idaho provenance (Priest River) produced slightly greater total volume by age 37 (415 m^3 per ha) than several coastal provenances from Washington and southwestern British Columbia (Lines 1976a). Periodic height measurements of an adjacent replicated test showed that this Idaho provenance was a slow starter, advancing in rank from 13th (of 14) at age 12 to 2nd at age 20. A Klamath, Oregon, provenance—the only representative of the Sierra-Cascade race in these older tests—ranked at or near the bottom in height growth. It had by far the greatest diameter relative to its height of any provenance, however, consistent with the diameter growth and stocky form of the Sierra-Cascade race in nature. In other British tests measured at 25 to 27 years, the largest volumes were produced by provenances from coastal Washington, the coast-interior transition in British Columbia, or a local forest of coastal origin (Forestry Commission 1967).

More recent tests in Britain and northern Ireland, including a wider selection of better identified provenances, gave mixed results at 3 to 9 years (Cannell 1974; Forestry Commission 1968, 1972, 1977; Lines 1976a; Savill 1976). Interactions were large, and no single provenance or group of provenances was superior. Oregon and Washington coastal origins were generally tallest; but on some sites, provenances from the coast of southern British Columbia, Vancouver Island, the Skeena River coast-interior transition, and the southern interior of British Columbia ranked near the top in height growth. The few Oregon Cascades provenances in these tests (LaPine, Cascadia) were among the slowest growing.

In Germany, where lodgepole pine is badly damaged by pine shoot moth *(Rhyacionia buoliana)*, relatively few provenances have been tested. At 15 years, a Washington coast provenance was tallest at several sites in West Germany, closely followed by Vancouver Island and interior British Columbia sources (Stephan 1976). Provenances from the southern Rocky Mountains and the Oregon Cascades were below average in height on all sites, and Sierra Nevada sources were uniformly the slowest growing.

In cold climates, the growth rate of provenances from the coastal region south of Alaska is reduced. A test largely confined to British Columbia and outplanted at two widely separated interior sites had high survival, but 5th-year increment of several coastal sources was only 61 to 83 percent of the plantation average (Illingworth 1975). Local sources showed no tendency to outperform more distant ones at 5 years, but by 9 years relatively local sources were performing better at both sites (British Columbia Forest Service 1977).

The relationship between early height growth and both elevation and latitude was evident in a British Columbia test of five widely distributed pairs of high- and low-elevation provenances grown at coastal and interior nurseries (Illingworth 1976a). Third-year height varied inversely with elevation and latitude in nearly all comparisons. An interesting exception—the slow growth of a pair of provenances from the north end of the Cascades—is consistent with the performance of Cascade-Sierra provenances in most other tests.

In the harsh continental climate of northern Sweden, height growth of the IUFRO collections showed little provenance × site interaction at 6 years: provenances south of about 51° latitude did badly at all sites (Lindgren and others 1976). Provenances with the greatest height growth were mostly clustered near 56° in northeastern British Columbia. California montane provenances predictably averaged slower height growth than any other group.

Many of the same IUFRO collections were represented in a test in southern Finland (Hahl 1978). At 8 years from seed, most interior provenances from 54° to 56° latitude in British Columbia were taller than more northern or southern interior provenances, and the best were 20 percent taller than select Scots pine origins in the test. The best provenances were matched in height growth by the offspring of trees planted in Finland in the 1920's and 1930's. These older tests sampled a limited range of provenances (Alberta and parts of southern British Columbia) that are probably suboptimal for Finnish conditions. On good sites under intensive management, however, they produced yields of 285 to 350 cubic meters per hectare at age 35 (von Weissenberg 1972).

Root growth has received much less attention than shoot growth, but 1st- and 2nd-year seedlings grown in Scotland were highly variable in the end-of-season ratio between root and shoot dry weight (Forestry Commission 1971). Provenance differences were large: southern coastal sources had the smallest root/shoot ratios and Glacier Bay—the most northern coastal population—had the largest. Comparable differences among a limited number of provenances were found by Cannell and Willett (1976) in an analysis of changes in this ratio during seedling development. These differences almost disappeared during shoot extension in the second season, but later reappeared. The authors concluded that a relatively greater investment in roots was associated with the shorter period of shoot elongation in high-elevation and high-latitude provenances.

The root/shoot ratio may influence tolerance to prolonged flooding (Vester and Crawford 1978). Provenances with the lowest ratios (south coast, coast-interior transition) suffered much higher mortality than high-latitude and interior sources.

Differences in the root/shoot ratio persist at least through the fourth growing season (Roberts and Wareing 1975). At this age, roots made up 14 and 20 percent of the plant's dry weight in two south-coastal sources, compared with 27 and 28 percent in Oregon-Cascade and Alberta sources. The root/shoot ratios of the coastal sources were significantly smaller.

Root development is of interest in Britain because of its probable relationship to a high incidence of windthrow and stem deformation in faster-growing provenances on many sites. At 11 to 30 years, south-coastal provenances had by far the highest frequency of trees with basal sweep, exceeding 70 percent on some sites (Moss 1971). Provenances from the interior wet belt of southeastern British Columbia and adjacent parts of the United States also showed moderately high frequencies of basal sweep on some sites. These data may exaggerate the problem, as Lines and Booth (1972) pointed out, because they include unspecified frequencies of trees with measurable but small deviations from the vertical. In another British study of a south-coastal provenance at 8 years, lean and basal sweep were significantly and positively correlated with tree height, branchiness, and a less extensive root system (Forestry Commission 1972). Coastal × interior hybrids produced in Britain were almost free of basal sweep at 6 years, but were comparable in height to a badly deformed south-coastal provenance (Lines and Booth 1972), suggesting one approach to the genetic improvement of this trait.

In a 6-year-old New Zealand test, stem lean (including basal sweep) was confined to central- and south-coastal provenances on a few exposed or hardpan sites.[5] Lean and height were weakly correlated, and one Puget Sound provenance (Shelton, Washington) combined moderately good height growth with a fairly low degree of lean.

Another factor influencing windfirmness and stem form is amount and pattern of branching. The coastal race tends to be branchier than inland races, independent of height growth rate. At 3 years, coastal provenances from Alaska (Skagway) to Oregon had more branches per plant (7.9 to 9.4) than central British Columbia or Oregon Cascade provenances (6.7), although the inland sources were taller than the Alaska source (Cannell and Willett 1976). At 9 years, accumulated branch length per centimeter of stem height was 18 and 19 centimeters in the same inland provenances, and 24 to 50 centimeters in the same range of coastal provenances (Cannell 1974). At 16 to 18 years, coastal provenances averaged 21 to 55 growing tips on a 6-year-old branch system, compared with 10 to 16 for inland provenances with almost the same range of heights (Lines 1966). In measurements based on the last five seasons' shoot growth of trees about 11 years old, a coastal provenance (Washington) had a larger proportion of its dry weight in branches (28 percent) than an interior British Columbia provenance (22 to 24 percent) and a correspondingly reduced proportion in stem (30 and 35 to 37 percent) (Thompson 1976).

---

[5] See footnote 3, p. 31.

Coastal origins tend to have larger branches, attached to the stem at smaller angles, than interior origins. In a 6-year-old New Zealand test, branches of the taller coastal provenances were uniformly longer, thicker, and more nearly vertical than the branches of Rocky Mountain-Intermountain and Sierra-Cascade provenances.[6] Branch length, thickness, and angle (measured from the horizontal) were strongly and positively correlated with each other and with height growth. Apart from the general trend, Rocky Mountain-Intermountain provenances rather consistently had smaller and flatter branches than the slower growing Sierra-Cascade provenances.

Coastal provenances also tend to have more branches in each whorl on the main stem. Two south-coastal sources in northern Britain had 6.0 and 6.2 branches per whorl, and an interior British Columbia source had 4.8 (Lines 1966). On a wide range of sites in New Zealand, coastal provenances from Puget Sound to California averaged 5 to 6.5 branches per whorl at 6 years, compared with 2.9 to 4.3 in Rocky Mountain-Intermountain and Sierra-Cascade provenances.[7]

Differences in the number of branch whorls produced each year are less consistent. South-coast provenances produce only a single whorl in Britain (Forestry Commission 1968, Thompson 1976). Coastal-interior transition (Skeena River) provenances have a high frequency of trees with more than one whorl (Lines 1966), and Queen Charlotte Islands provenances have more whorls than coastal provenances to the north and south (Thompson 1976). In New Zealand, however, coastal provenances had nearly as many whorls as inland provenances on an array of sites, and one Oregon-coast source had among the highest frequencies of extra whorls, averaging 1.4 whorls annually.[8] In Scotland, trees producing two whorls had 72 percent more primary branches and a greater height increment in 2 successive years (plus 26 and 7 percent) than single-whorled trees of the same inland origin (Thompson 1976).

Repeated stem forking appears to be under genetic control in British provenance tests (R. Lines, pers. commun., June 1978). Provenances from the southern interior of British Columbia have a much higher incidence of repeated forking than central British Columbia or Cascade provenances.

The branchier crowns of coastal trees tend to have larger numbers of leaves. At 9 years, three coastal provenances (Alaska to Oregon) had 19,000 to 56,000 needle-pairs per tree, while interior British Columbia and Oregon-Cascade trees averaged only 11,000 (Cannell 1974).

Differences in height increment among provenances are more closely related to the number of leaves on the annual extension of the leader than to leaf spacing or photosynthetic efficiency (Cannell 1976b, Roberts and Wareing 1975). Shoots of 3-year-old trees of two south-coastal and two interior origins did not differ significantly in internode length, but the fascicles of 9- to 10-year-old coastal trees were consistently more closely spaced than those of interior trees (Cannell 1974, 1976b). At 10 years, internodes of three coastal provenances (Alaska to Oregon) were 1.06 to 1.14 millimeters long, Oregon Cascades 1.18 millimeters, and interior British Columbia 1.35 millimeters (Cannell 1976b). First-year seedlings of two coastal and two inland provenances differed significantly in net photosynthetic rate and relative leaf weight (expressed as a percent of plant weight), the two coastal sources having the highest and lowest values of both variables (Sweet and Wareing 1968). These factors were negatively correlated, and all four provenances had nearly identical relative growth rates in their first season. It is uncertain, however, to what extent these relationships, based mostly on primary leaves, are applicable to the secondary leaves (needles) of older plants.

Compared to interior provenances, most coastal provenances produce more leaves on the annual shoots of their leaders or vigorous upper branches (table 5).

One factor influencing shoot growth is the duration of apical activity, and this varies strikingly during the first season of growth in the greenhouse (Critchfield 1957, Sweet and Wareing 1968):

---

[6] See footnote 3, p. 31.

[7] See footnote 3, p. 31.

[8] See footnote 3, p. 31.

Region	Days from germination to terminal-bud formation	
	Mean	*Median*
South coast	160-230	165, 215
Alaska coast	116	
Sierra Nevada	130-147	
Oregon Cascades		145
Yukon to Colorado	81-110	
Alberta		120

The fairly prolonged growth period of Sierra-Cascade origins, in contrast to their slow growth in older tests, suggests that the duration of first-season shoot growth is not a close indicator of subsequent height growth.

Table 5.—*Leaf production on annual shoots of lodgepole pine*

	Provenance		Pairs of needles or primordia	
Age	No.	Region		Reference
3	2	South Coast	394, 471	Roberts and Wareing 1975
	2	Rocky Mts., Oreg. Cascades	196, 206	
3	4	Coast (Alaska-Oreg.)	220-315	Cannell 1976a
	3	Interior B.C., Oreg. Cascades	228-251	
9	3	Coast (Alaska-Oreg.)	320-475	Cannell 1976b
	2	Interior B.C., Oreg. Cascades	229, 225	
10	2	Alaska, Oreg. coast	189, 248	Cannell and Willett 1975
	2	Interior B.C., Oreg. Cascades	169, 178	

After the seedling stage, the number of needles on the annual shoot is determined by the rate and duration of leaf initiation in the bud during the preceding season. In their third growing season in Scotland, a wide range of coastal and interior provenances initiated a maximum of 2.2 to 3.2 lateral appendages per day (Cannell 1976a). At 10 years, most provenances had lower maximum rates, with a range of 1.5 to 3.2 appendages per day (Cannell and Willett 1975). At both ages, most coastal origins had higher maximum initiation rates than interior origins, and Oregon-coast provenances had the highest rates. Initiation rates peaked between late June and early August, and southern coastal provenances continued to initiate appendages later in the season than other provenances.

The number of needles in the terminal bud influences both the rate and duration of extension growth in the following year (Cannell and others 1976), but the onset of shoot elongation is controlled by other factors. In an 8-year-old test in central Sweden, high-latitude inland provenances were about 10 days ahead of a Vancouver Island provenance at all stages of elongation (Hagner and Fahlroth 1974). By early June, elongation was 58 to 68 percent complete in provenances north of 57° latitude, and 42 to 58 percent complete in Canadian provenances south of 57°. In three seasons, an interior British Columbia provenance in Scotland completed 50 percent of its height growth 12 to 24 days earlier than a Washington coastal source (Thompson 1976). Although the coastal trees began growing later in the season, their total period of elongation was 29 and 40 percent longer in two seasons.

The same pattern was evident in comparisons of 10- and 11-year-old trees of six widely distributed interior and six coastal provenances on two sites in northern Britain (Cannell and others 1976). Interior provenances began to elongate earlier than coastal provenances (Alaska to Oregon), peaked earlier, and slowed down long before the central- and south-coastal sources. Northern and southern coastal sources peaked at the same time, but the southern group grew faster throughout the season, had a higher maximum rate of growth, and continued to elongate 2 to 6 weeks after all other provenances.

Needles

The needles emerge from the bud after shoot growth is well underway, and grow in length from a basal meristem. In Scotland, needle elongation was 50 percent complete about a month after the stem had reached this stage (Thompson 1976). Needle elongation was about 3 weeks earlier in interior British Columbia provenances than in south-coastal sources (Thompson 1976, Cannell and other 1976). Among coastal sources in Scotland, needle elongation ceased in a smooth latitudinal gradient, with an Alaskan source terminating about a month before a California source (Cannell and others 1976). Some interior provenances extend their needles more rapidly than coastal provenances (Cannell and others 1976), and most have longer needles by the end of the season.

Racial differences in needle dimensions are generally more clear-cut in provenance tests than in natural populations, but seedling stages are an exception. The needles (secondary leaves) of first-year greenhouse-grown seedlings of south-coastal provenances were about the same length as those of their parents in natural stands, but interior seedlings—in a reversal of the situation in nature—had shorter needles than coastal seedlings and much shorter needles than their parents (Critchfield 1957). All seedling needles were more slender than those of their parents, but Sierra Nevada provenances had the widest needles.

Second-year seedlings, in contrast, produce needles that are much longer than those of older trees. In a range-wide provenance test on Vancouver Island, mean needle length was 7.2 to 10.2 centimeters (Illingworth 1975)—longer than in natural populations. Sierra-southern Cascade needles were shortest (7.2 cm), and provenances in the interior wet belt of British Columbia had the longest needles (10.2 cm). All other inland provenances had needle lengths of 8.2 to 9.5 centimeters, a little longer than coastal provenances (8.0 to 9.1 cm). A Norwegian test including many provenances gave similar results (Dietrichson 1970). Only in a few California sources (Mendocino, Sierra Nevada) were needle lengths comparable to natural stands (4.5 and 6 cm). All other sources had much longer needles (8 to 14 cm).

Older trees (16 to 28 years) at Placerville, Calif., (Critchfield 1957) and in northern Britain (Jeffers and Black 1963, Critchfield 1957, Lines 1966, 1976a) had shorter needles, and the distinction between coastal and inland provenances was sharp. In 3 years of measurements in Scotland, needle length averaged 4.4 to 5.3 centimeters in central- and south-coast provenances and 5.4 to 7.3 centimeters in inland provenances, with a single Oregon-Cascade source having slightly shorter needles (5.4 to 6.6 cm) than other inland sources (5.9 to 7.3 cm). Needle length varied as much as 20 percent between years, but provenance ranking tended to be the same.

Differences in needle width are also more discrete in provenance tests than in natural stands. In a northeast Scotland plantation measured by Jeffers and Black (1963) and Lines (1976a), coastal needles averaged 1.34 to 1.50 millimeters in width, Rocky Mountain-Intermountain needles 1.51 to 1.61 millimeters, and a single Oregon-Cascade provenance 1.85 and 1.77 millimeters. Southern Cascade-Sierra Nevada provenances also had consistently wider needles than the rest of the species in northern England, New Zealand, and California (Critchfield 1957). The influence of environment was evident in the wider needles of two British Columbia sources grown in New Zealand, compared with the same provenances in England.

Needle volume and dry weight also exhibit discrete differences. Needle-pair volume was 75 to 83 cubic millimeters in three coastal provenances (Alaska to Oregon) grown in Scotland, compared with 90 and 109 cubic millimeters in single British Columbia and Oregon-Cascade provenances (Cannell 1974). Coastal x interior hybrids were similar in volume to coastal provenances. Needle weight increased in this sequence: north coast, south coast, interior British Columbia, south-central Oregon, and Sierra Nevada, with highly significant differences between groups (Forestry Commission 1970, 1976; R. Lines, pers. commun., June 1978).

Like needle size, density of stomata showed sharper regional differences in a common environment than in natural stands, although this comparison was confounded with tree age (Illingworth 1975). The number of stomata per square millimeter on the flat face of the needle was lower in 2-year seedlings than in their parents in natural stands, and big differences between interior British Columbia stands almost disappeared in two nurseries. In one, two coastal sources had 47 to 51 stomata per square millimeter compared with 34 to 39 for three inland sources, and in the other the numbers were 40 (coastal) and 30 to 33 (inland). In a nursery test including 140 provenances, coastal provenances averaged 45 to 52, southern Cascades-Sierra 39, and all other interior groups 34 to 38 stomata per square millimeter.

The concentration of nitrogen, phosphorus, and potassium in the needles differed markedly among provenances in Scotland (Forestry Commission 1970). A fast-growing Washington-coast provenance was lowest in nitrogen, and it and more northern coastal and transitional provenances were lowest in phosphorus and highest in potassium. A slow-growing Oregon Cascade provenance was highest in nitrogen and phosphorus and low in potassium. It is not clear how these concentrations relate to nutrient levels needed for optimum growth, but Lines (1966) suggested that coastal and inland races may differ in nutrient requirements.

In those instances where comparisons are possible, the number of resin canals in the needles is similar in provenance tests and natural stands (Critchfield 1957, Jeffers and Black 1963, Lines 1976a). The number of resin canals decreased from the base to the tip of the needle in most provenances, but in provenances from southeastern British Columbia and northern Idaho the number increased (Black 1963b).

Wood, Bark, and Resin

Wood properties appear to be strongly influenced by environment, and provenance differences are not usually consistent with what little is known of variation in natural stands. In a detailed comparison of single south-coastal and interior British Columbia provenances in Scotland, the coastal trees had significantly more summerwood and higher wood density, as they do in natural stands, as well as shorter tracheids (Henderson and Petty 1972). However, in another study of the same plantations, several coastal and interior provenances had about the same range in percentage of summerwood (Jeffers and Black 1963). Coastal and interior provenances showed no consistent differences in wood properties on several sites in New Zealand, although some interior provenances were unexpectedly higher in percentage of summerwood and resin content (Harris 1971). Two New Zealand land-races of coastal origin differed consistently in wood density on several sites. In Finland, British Columbia trees had a greater percentage of heartwood than Alberta trees—probably because of their greater size—and a smaller percentage of bark (Hakkila and Panhelainen 1970). Differences in cellulose and lignin content among two coastal and two inland provenances in Bavaria were small, although one inland provenance (British Columbia) was higher in lignin than the other inland (Oregon) or one coastal provenance (Schütt 1958). Anatomical features of the wood showed no consistent differences among several coastal and inland provenances (Black 1963a).

Bark is not a good diagnostic character in plantation-grown trees (Lines 1957). In one plantation in Scotland, several inland provenances (southeastern British Columbia and the adjacent United States) had thicker bark than central- and south-coastal provenances (Lines 1976a).

Wood resin has not been studied in provenance tests, but Forrest (1977) analyzed the cortex resin of 4- to 19-year-old trees in many provenances growing in Britain. The level of β-phellandrene was highest (82 percent) in north-coastal provenances, decreasing gradually to the south and more abruptly inland. Within the inland region, it decreased from west to east, and reached its lowest level (15 percent) in the single Sierra Nevada provenance analyzed. Camphene exceeded 1 percent only in a cluster of central British Columbia provenances (2.3 percent) and two provenances on the coast of southern Oregon and northern California (3.6 percent). Carene reached high levels in Alberta, and a single Mendocino (California) provenance had much more carene than other coastal provenances. The greatest variability between provenances was in the Vancouver Island-Puget Sound region, and the greatest within-provenance variability was in interior British Columbia.

Reproductive Characters

Provenance differences in flowering were described elsewhere. (See "Sexual Reproduction.") In summary, meiosis and flowering are earlier in interior provenances than in coastal provenances, and Mendocino White Plains trees are later. Both coastal and White Plains trees may be protogynous, but interior trees are not. White Plains trees are much heavier pollen producers than coastal trees. Reproductive abnormalities are more common in interior provenances. Differences in cone-opening between White Plains and coastal provenances persist in a common environment.

Northern coastal provenances began to produce cones at an earlier age than southern provenances in New Zealand[9] and Britain (Lines

---

[9] See footnote 4, p. 31.

1977). At 6 years, 14 to 47 percent of trees from Oregon to Vancouver Island were producing cones in New Zealand, compared with only 2 percent of trees from the California coast and Mendocino White Plains.

Cone density was more uniform in provenance tests than in natural stands, and in Britain and New Zealand only the lower-density cones of an Oregon-Cascades provenance were very different from the cones of other provenances (Critchfield 1957). New Zealand trees had denser cones than trees of the same provenances grown in Britain. One New Zealand land-race (Waiotapu) has serotinous cones (Harris 1971), but in Britain the serotinous habit was just beginning to show up in Alberta provenances at 45 years (Lines 1977).

Variations in cone orientation in British provenance tests indicate that this characteristic is strongly inherited (R. Lines, pers. commun., June 1978). Coastal provenances have strongly reflexed cones, and the highest frequency of semierect cones is in provenances from Alberta and the southern interior of British Columbia.

A few coastal and interior provenances grown in Britain were similar in seed size, with one exception: an Oregon-Cascade provenance had larger seeds (Jeffers and Black 1963). Seed weight of a larger number of provenances in Britain was more variable, and corresponded in a general way to regional variations in natural populations (R. Lines, pers. commun., June 1978).

Pests and Air Pollution

In Ireland, damage to foliage by the sawfly *(Diprion pini)* was more severe on the slower-growing inland provenances than on coastal trees (Lines 1957). Another insect, the pine shoot moth *(Rhyacionia buoliana)*, damaged coastal provenances more severely in Denmark (Feilberg 1964) and West Germany (Stephan 1976). The amount of damage varied greatly among sites in Germany, but two coastal provenances consistently suffered more damage than the widely scattered inland provenances. Damage by this insect is a critical problem in the Netherlands, and the fastest growing provenances—both coastal and interior—are the most severely damaged (Kriek 1976).

In Scotland, provenances artificially inoculated with a canker-forming fungus *(Crumenula sororia)* varied widely in susceptibility, but much of the variation was unrelated to region of origin (Hayes 1975). The susceptibility of Alberta and Sierra-Cascade provenances was confirmed by observations of plantations, and south-coastal provenances were moderately resistant. However, in other parts of the range, interior British Columbia in particular, there were large, significant differences between provenances in the same region.

In a nursery in interior British Columbia, the shoot blight *Sirococcus strobilinus* infected and sometimes killed 2 to 10 percent of 1st-year seedlings from the interior wet belt of British Columbia, the Cascades, and the Sierra Nevada (Illingworth 1973). Seedlings of coastal, northern, and eastern provenances were less susceptible, with less than 1 percent infection.

A New Zealand test showed a remarkably steep gradient among coastal provenances in damage by the introduced opossum *(Trichosurus vulpecula)*[10]. The southernmost of three California provenances had 98 percent damage, decreasing to 57 percent in the northernmost. More northern provenances (Oregon to Vancouver Island) suffered much less damage: 4 to 21 percent. Four New Zealand provenances of coastal origin had the same high levels of damage as the southernmost California sources (87 to 98 percent).

Another striking sample of differential animal damage was noted by von Weissenberg (1972) in a test of IUFRO provenances in Finland. Hares killed all trees of a provenance from the southern California mountains, while the other 20 provenances—all from Canada—were undamaged.

In Germany, foliage of one Saskatchewan and two Alberta provenances was significantly less damaged by sulfur dioxide, a common industrial air pollutant, than foliage of other inland provenances (Tzschacksch and others 1969). First-year seedlings of a Washington coastal provenance were more severely damaged than seedlings from the Oregon Cascades, Idaho, and Wyoming (Lang and others 1971).

---

[10] See footnote 4, p. 31.

Local Variation

In addition to broad regional trends, provenance tests sometimes provide evidence of ecological races or ecotypes, usually associated with localized edaphic conditions. Most of the local races identified in lodgepole pine are in the coastal region.

"Mendocino" sources in some provenance tests cannot be assigned to the White Plains or the nearby coast, but in a 6-year-old New Zealand test a White Plains provenance produced only 55 to 63 percent as much volume as California coastal provenances to the north and south[11]. However, it is uncertain whether slower growth is typical of the White Plains race. The largest trees of lodgepole pine in cultivation, growing in western Ireland, were probably of White Plains origin (Hanan 1963). They had reached maximum heights of 102 feet (31 m) and diameters of 3 feet 5 inches (1 m) at 75 to 80 years before some of them were blown down in a gale. In small-scale field tests in California, planted trees grown from White Plains seed survived and grew better on a White Plains site than trees of several other provenances, including the nearby coastal bluffs (McMillan 1964). The coastal trees were completely eliminated between 2 and 13 years after outplanting on the White Plains. Wildlings transplanted from the coast to the White Plains had low survival and poor growth, and the survivors retained their open-cone habit.

Provenances from ultramafic soils in the mountains of Del Norte County, California, were intermediate in growth between south-coastal and inland provenances in several tests (New Zealand: Cunningham and Roberts 1970,[12]; northern Ireland: Savill 1976). In its cortex monoterpenes, however, the group resembled south-coastal provenances more closely than it did the Sierra-Cascade race to the east (pers. commun., R. Lines, Aug. 1977).

Lodgepole pine also grows on ultramafic soils at several places in the Cascades and Puget Sound region of northwest Washington, and Kruckeberg (1967) suggested that it is locally adapted. Three ultramafic provenances were significantly taller than two non-ultramafic provenances after 38 months of growth on an ultramafic soil, but growth was not compared on non-ultramafic soil.

Evidence for distinct muskeg and sand-dune ecotypes in the central coastal region was presented by Shelbourne and Miller[13]. They interpreted the Queets provenance, from a peat bog in western Washington, as a southern outlier of a slow-growing but straight-stemmed muskeg ecotype on the west coast of Vancouver Island and farther north. Supporting this interpretation, the cortex monoterpenes of the Queets provenance were like those of muskeg provenances to the north, and unlike those of provenances from coastal dunes farther south (pers. commun., R. Lines, Aug. 1977).

Land-Races

Naturalized strains, or land-races, of tree species grown outside their natural range sometimes outgrow comparable provenances introduced directly from the native range of the species. This competitive edge is probably compounded of one or more generations of natural selection plus wide outcrossing. In Finland, a group of land-races that had originated in the southern part of western Canada was 11 percent taller at 8 years than a comparable group of Canadian provenances and about equalled in height the tallest group of provenances, which originated farther north in Canada (Hahl 1978).

In less stringent environments, land-races of lodgepole pine are not necessarily superior to natural provenances—at least in the environments to which they have presumably adapted. Irish provenances, mostly of coastal origin, were generally equal, but not superior, to south-coastal provenances in 5- to 8-year-old tests in Ireland (O'Driscoll 1972, Savill 1976). However, at two sites in the Netherlands, a few of the many Irish provenances tested were growing faster at 9 to 11 years than any south-coastal provenance in the tests (Kriek 1973, 1976). Local provenances in Britain display no consistent superiority in either growth rate or form (Forestry Commission 1967, Lines 1976a).

---

[11] See footnote 4, p. 31.

[12] See footnote 4, p. 31.

[13] See footnote 4, p. 31.

Two of the better known land-races in New Zealand are the second- and third-generation Kaingaroa and Waiotapu strains, both probably of coastal origin. These and other New Zealand land-races of coastal origin have generally matched, but not excelled, the fast-growing south-coastal provenances in growth and form (Miller 1969,[14, 15]). Remarkably, the Kaingaroa strain equalled or surpassed in height growth the fastest-growing south-coastal provenance 3 years after outplanting in Scotland (Lines 1976a) and Ireland (O'Driscoll 1972).

---

[14] See footnote 3, p. 31.

[15] See footnote 4, p. 31.

Controlled Hybridization

Except for *Pinus banksiana* and *P. virginiana*, all attempts to cross *P. contorta* with other pines have been unsuccessful. Many attempts to cross this species with *P. sylvestris* of subsection Sylvestres have yielded only hollow or ungerminable seed (Brown 1970, Duffield 1952, Ehrenberg and others 1955). Early reproductive breakdown is indicated by increased conelet abscission (Hagman 1964) and greatly reduced numbers of hollow seed (Brown 1970). A few crosses with other species in Sylvestres have also failed (Duffield 1952; unpublished data, IFG). Unsuccessful crosses have also been attempted with other western American pines, including the sympatric *P. jeffreyi*, *P. muricata*, and *P. washoensis*, and the allopatric *P. coulteri* and *P. radiata* (Duffield 1952; Unpublished data, IFG).

In recent crosses at Placerville, one of several *P. virginiana* pollen parents yielded many germinable seeds in crosses with any of several Sierra lodgepole females. The offspring were definitely hybrids: most seedlings were chlorotic and dwarfish, unlike their lodgepole half-sibs, and many died not long after germination (Unpublished data, IFG).

The first successful controlled cross between *P. contorta* and *P. banksiana* was made in 1939 on a native Sierra Nevada lodgepole pine. The hybrids were described and named *P. murraybanksiana* by Righter and Stockwell (1949). This cross has been repeated many times on Sierra Nevada trees, usually with considerable success. Of 37 crosses with jack pines of varied geographic origin, all accompanied by within-species control crosses, 31 produced germinable hybrid seed. Average crossability (seed yield relative to within-species yield) was 31 percent, a moderately high level compared with other species combinations in *Pinus*.

Despite the close relationship of the parent species, some F_1 and advanced-generation hybrids produce a larger percentage of aborted pollen than any other pine species or hybrid so far investigated (Saylor and Smith 1966). In the first F_1 progeny, Righter and Stockwell (1949) reported 40 to 50 percent aborted pollen, and Saylor and Smith (1966) found 0.5 to 27.5 percent. In a large number of F_2 and F_3 hybrids derived from this progeny, Saylor (pers. commun., Feb. 1972) encountered pollen abortion levels of 0 to 42 percent. High percentages of aborted pollen are not confined to this family: one or more natural hybrids also produced 50 percent aborted pollen (Moss 1949). Pollen abortion is not, however, a general property of lodgepole × jack pine hybrids; several F_1's in other unrelated families produced at Placerville all had less than 2.2 percent aborted pollen (Saylor and Smith 1966; Saylor, unpublished data). It is possible that pollen abortion is under simple genetic control, segregating in the haploid pollen. This is suggested by (1) the presence of either high (> 22 percent) or low (< 4 percent) levels of abortion in nearly all trees of the affected lineage, and (2) the apparent lack of relationship between the amount of aborted pollen and the amount of meiotic irregularity (Saylor and Smith 1966; Saylor, unpublished data).

Despite these levels of aborted pollen, F_1 to F_3 hybrids produce some sound seed in most combinations (Righter and Stockwell 1949, unpublished data, IFG). The presence of more than one egg in the female gametophyte, providing a margin for reproductive error, may explain the failure of aborted pollen to markedly influence hybrid reproductive capacity (Righter and Stockwell 1949).

Hybrids of Sierra Nevada lodgepole pine and jack pine are poorly adapted to the native range of jack pine. Backcrosses of F_1 hybrids to jack pine suffered relatively heavy winter injury in northern Ontario at 7 to 8 years (Yeatman and Holst 1972). In northern Wisconsin, winter injury to the foliage of 6-year-old hybrids and hybrid derivatives was roughly proportional to the genetic contribution of Sierra lodgepole pine (Rudolph and Nienstadt 1962). At several sites in the Great Lakes region, F_1 hybrids were more susceptible than jack pine to sweetfern and eastern gall rusts (Anderson and Anderson 1965).

The performance of lodgepole × jack pine hybrids is somewhat better in the northern Rocky Mountains. Field tests in Montana and Idaho were assessed by Lotan (1967b) and Rehfeldt and Lotan (1970), most recently at 17 to 20 years. Genotype-site interactions were large, and neither California nor Montana hybrids with jack pine exhibited any clear-cut superiority to northern Rocky Mountain lodgepole pine in height and diameter growth. In these tests and at

Placerville, Sierra Nevada lodgepole pine was slower growing than the hybrids, jack pine, or Rocky Mountain lodgepole pine.

Differences between lodgepole and jack pines in turpentine composition segregated in the F_2 and F_3 hybrid and backcross generations, suggesting that the differences are controlled primarily by a limited number of major genes (Zavarin and others 1969). All F_1 hybrids had β-phellandrene in their turpentine, but some F_2 and F_3 hybrids and most backcrosses to jack pine lacked β-phellandrene and had turpentine consisting mostly of pinenes.

No significant genetic barriers have been encountered in crosses between geographic races of lodgepole pine. Hybrids of the coastal (including Mendocino White Plains) and Sierra Nevada races have desirable attributes as Christmas trees in some environments. These hybrids were produced and tested on a large scale in a breeding program financed by the California Christmas Tree Growers Association (Critchfield 1965). In a total of more than 100 crosses in both directions between trees of coastal origin at Placerville and Sierra Nevada trees in natural stands, interracial and intraracial crosses yielded nearly equal amounts of sound seed.

Crosses between coastal and inland races have been made on a fairly large scale in Britain, with the objective of combining the greater vigor of south-coastal trees and the straighter stems, narrower crowns, and finer branches of inland provenances, mostly in interior British Columbia (Forestry Commission 1969, 1970).

Cytogenetics

Like all other pines, lodgepole pine is remarkably uniform in chromosome number and morphology. It has a diploid complement of 24 large chromosomes, and the karyotype closely resembles that of other species in subsection Contortae (Saylor 1972). Trees of coastal and interior (Montana) origins growing in coastal British Columbia had a haploid chromosome number of 12, determined at meiosis (Ho and Owens 1974). Nuclear size and amount of nuclear DNA are also constant (Teoh and Rees 1976). Root tips of seedlings from nine widely scattered localities (interior and coastal-interior transition of British Columbia, and Oregon Cascades) showed no significant variation in either feature.

Trees of coastal and inland sources growing in Sweden had a low frequency of chromosomal irregularities at meiosis (Ekberg and others 1972). On the British Columbia coast, Montana trees had a higher frequency of meiotic abnormalities (4.3 percent) than native shore pines (1.5 percent), and the pollen of one Montana tree also had a high frequency (12 percent) of abnormalities in size or structure (Ho and Owens 1974).

Meiotic irregularities were more common in lodgepole and jack pines and their F_1 hybrids growing at Placerville (Saylor and Smith 1966). The most frequent were precocious disjunction, univalents, lagging chromosomes, inversion bridges, and micronuclei. Among F_1 to F_3 hybrids, high levels of meiotic irregularities were about equally frequent in trees with high (> 20 percent) and low (< 4 percent) levels of aborted pollen (L. C. Saylor, pers. commun., Feb. 1972).

A few triploid seedlings were produced from crosses between two untreated trees and a 28-year-old tree that had been treated with colchicine as a newly germinated seedling (Johnsson 1975). Meiosis was fairly normal in the treated tree, although lagging chromosomes were common. Its pollen grains had 24 or 48 chromosomes, and about 20 percent had an extra air sac or other abnormality. The triploid seedlings all died soon after germination, and it was not fully established whether they actually had three complete sets of chromosomes.

Genetic Improvement

Many attributes of lodgepole pine make it well suited for use in genetically improved, short-rotation plantations managed intensively for fiber or solid wood. Selection is simplified by the typical occurrence of the species in extensive, even-aged stands with substantial tree-to-tree variability (Illingworth 1975). Most strains have relatively rapid early growth; the Sierra-Cascade race is an exception. Pollen and seed are produced early in life, regularly, and abundantly; a large proportion of the strobili develop into cones; cone and seed predators are not a major problem; and the seed germinates readily and completely. Where serotinous cones are present, seed is available throughout the year. Vegetative propagation is not difficult. Hybridization of provenances and races is easy, with no known genetic barriers between populations.

Within the native range of lodgepole pine, these advantages were outweighed by low economic values until about 1970. In British Columbia, the species was hardly planted until the mid-1960's, but by 1972 8 million seedlings were planted annually in the interior (Illingworth 1975). With its extensive forests of interior lodgepole pine, British Columbia has the most elaborate and advanced lodgepole improvement program in North America. Unlike most efforts aimed at the improvement of a native species, this program has emphasized provenance testing. In 1974, subsets of a total of 150 provenances were planted at 60 locations throughout the interior of the Province[16]. Individual tree selection was begun in 1974 (fig. 4). By 1979 it was completed in four well-defined "selection units": areas with good access, more productive sites, and often a high frequency of non-serotinous cones and a greater regeneration problem (Illingworth 1975, Wheeler 1979). In 1974 a grafted clonal seed orchard derived from part of interior British Columbia was established (Industrial Forestry Association 1978). Survival of grafts from trees selected in the Prince George region averaged 47 percent by late 1976, with much better success in the greenhouse than in the field (British Columbia Forest Service 1977). In northern British Columbia and the Yukon, field selection is a joint effort with Swedish organizations (N. Wheeler, pers. commun., Jan. 1977). Estimates of the heritability of 3d-year height, based on 124 families from 10 British Columbia localities, are encouragingly high: 0.57 and 0.23 at two widely separated nurseries (Illingworth 1976a).

The most advanced program in the United States is that of the Weyerhaeuser Company in south-central Oregon. Begun in 1970, it includes about 1,200 trees, mostly 10 to 40 years old, selected at low intensity and grafted into a clonal seed orchard remote from natural stands (Blackman 1978, J. D. Daniels, pers. commun., Marc 1978). Much of the breeding (a disconnected partial diallel scheme) has been completed for progeny tests of the select trees.

Figure 4.—Select tree growing in the Nilkitwa drainage, abou 50 miles north of Smithers, British Columbia (photo b N. C. Wheeler).

---

[16] Wheeler, N. The lodgepole pine improvement program in British Columbia. Presented at West. For. Genet. Assoc. Meet., 1976.

The Forest Service has initiated improvement programs in its Northern (northern Idaho, Montana) and Pacific Northwest (Washington, Oregon) Regions. In the Northern Region, open-pollinated seed for progeny testing is collected from about 50 trees selected at low intensity (1 in 50 to 100) on each National Forest. The trees are concentrated in a few good stands, with 5 to 10 select trees in each stand. Seedling seed orchards will ultimately be produced from crosses of the better families in the progeny tests (Howe 1973, [17]). The Pacific Northwest Region has emphasized the development of methods for screening seedling progenies for resistance to western gall rust, a serious disease that exhibits great tree-to-tree variation in natural stands. A trial run for large-scale screening was successfully completed in 1976 (Industrial Forestry Association 1975, 1977).

Outside the native range of lodgepole pine, provenance selection has been supplemented in recent years with other approaches to improvement. In New Zealand, where lodgepole pine has a minor role for planting on difficult sites, a selection program begun in the late 1960's is based on two local land-races of coastal origin (Miller 1969). These strains have matched the best of the southernmost coastal provenances in early testing, and may have originated in the same optimum region. About 100 trees of each strain were selected at the relatively high intensity of 1 in 2,000. Open-pollinated progeny of select-tree grafts will be tested on harsh sites. Future alternatives include conversion of a progeny test into a seedling seed orchard or establishment of a clonal seed orchard from progeny-test results. Ultimately the program's genetic base may be broadened to include trees of known provenances now being tested.

The improvement programs of Great Britain and Ireland, similar in many respects, were expanded to include approaches other than provenance-testing in about 1960 (Faulkner 1974, O'Driscoll 1972). Both countries have set aside selected "seed stands," sometimes thinned and fertilized, to ensure an adequate, reliable supply of seed of known provenance.

Individual tree selection began in the 1960's. In Britain, 663 phenotypically superior trees had been identified by 1971 and most had been grafted into a clone bank (A. M. Fletcher, pers. commun., Jan. 1972). Most of the select trees are in British stands, but a sizable fraction were selected in Ireland and Denmark. The first selections were usually 25 years or older, but more recently younger trees have been included. The main criteria for selection are stem straightness and volume growth. Selection intensity in these planted stands has varied from low to moderate at the start to much higher in recent years (Faulkner 1974). By 1970 Britain had established 11.5 hectares of grafted clonal seed orchards (Faulkner 1974), and Ireland 6 hectares (O'Driscoll 1972).

The first interprovenance hybrids were produced in Britain in 1961 (A. M. Fletcher, pers. commun., Jan. 1972). This approach presents fewer problems outside the native range of a species, where loss of local adaptedness is not a consideration. Its potential is greatest in a country like Britain, where a considerable range of provenances with quite different characteristics grow fairly well. The primary objective, combining the better stem form and greater windfirmness of slower-growing interior and north-coastal provenances with the faster growth of the poorly formed, unstable south-coastal provenances, was partly fulfilled by the first coastal × interior hybrids produced (Forestry Commission 1976). More ambitious goals for a crossing program among provenances are suggested by the analyses of shoot-growth components done by Cannell and his associates. They concluded that maximum gains in height growth are unlikely to be achieved by selection, either between or within provenances, because the most important components of shoot growth do not occur together naturally (Cannell and others 1976). These components include: initiation of apical growth early in the growing season (northern and interior provenances), cessation of apical growth late in the season (south-coastal provenances), rapid rates of lateral-appendage production (many coastal provenances), and long internodes (some interior provenances). The eastern Washington × south-coastal British Columbia hybrids studied by Cannell and Willett (1975)—apparently among the earliest interprovenance hybrids produced in

---

[17] Steinhoff, R. J. 1974. Work plan for a lodgepole pine improvement program, prepared for Region 1 USFS. Intermt. For. and Range Exp. Stn., Moscow, Idaho.

Britain—successfully combined some of these characters and equalled a fast-growing Oregon-coast provenance in needle production.

In Scandinavia and Finland, where lodgepole pine does well on good sites in some regions, three contrasting approaches have been taken to genetic improvement. In Norway, where considerable information is available from provenance testing, seed has been imported from 10 selected stands in northern British Columbia (Dietrichson 1976). Progeny of these stands will be planted in large blocks on many sites, and individual tree selection will be done in the plantations. The British Columbia seed will also be used to establish seedling seed orchards.

A selection program in Finland is based on mature trees in older provenance tests. Although these tests were mostly confined to Alberta and a limited area in southern British Columbia, it has been concluded that the provenances suited to Finnish conditions are relatively well known (Tree Breeding Committee [Finland] 1976). By 1971, 236 trees representing eight known provenances had been selected in southern Finland (Von Weissenberg 1972). Many were propagated in 1972, and both seedling and grafted-clonal seed orchards have been established. Selection is confined to disease-free stands with good growth and form, and standards are high: in comparisons with 20 dominant trees in the stand, selection differentials are 5 to 10 percent in height and 25 to 33 percent in volume. Recent provenance tests are mostly planted in northern Finland, but height growth of one 8-year-old test of IUFRO provenances in southern Finland indicated that the best Canadian provenances are near 55° latitude—farther north than most provenances in the older tests (Foundation for Forest Tree Breeding 1977, Hahl 1978).

In contrast to the Finnish approach of emphasizing trees that have grown to maturity within the country, two companies in Sweden (Swedish Cellulose Company and Stora Kopparberg), in cooperation with the University of British Columbia and several government agencies, have selected phenotypically superior trees in northern British Columbia and the Yukon for use in central and northern Sweden. Select trees were in high-quality, disease-free, accessible stands, mostly more than 50 years old. Between 1970 and 1974, cones and scions were collected from 184 selected and felled trees, and grafting was done in both Sweden and British Columbia (Hagner 1971, Sziklai 1976). The clonal seed orchards in Sweden should, at a minimum, produce seed of provenances that are better matched to Swedish conditions than the more southern Canadian provenances in older Swedish tests. Whether progeny grown in Sweden from parents selected in Canada will also incorporate an increment of genetic gain from phenotypic selection has been questioned by other Swedish workers (Ekberg and others 1972).

Acknowledgments

Many North American and European scientists generously made available their unpublished data or other information on lodgepole pine. Their contributions are noted in the text as personal communications, but the information supplied by Keith Illingworth, LeRoy C. Saylor, and Christopher C. Smith warrants special mention. The manuscript was greatly improved by the comments of Lauren Fins, David E. Harry, Keith Illingworth, Roger Lines, James E. Lotan, and Connie I. Millar.

Literature Cited

Achuff, P. L., and G. H. La Roi.
1977. *Picea-Abies* forests in the highlands of northern Alberta. Vegetatio 33:127-146.

Ackerman, R. F.
1966. Effect of storage in slash on quantity and quality of lodgepole pine seeds available for regeneration. Can. For. Br., Alberta/Territories Reg. For. Res. Lab., Inf. Rep. A-X-3, 22 p., Calgary.

Ackerman, R. F., and J. L. Farrar.
1965. The effect of light and temperature on the germination of jack pine and lodgepole pine seeds. Univ. Toronto, Fac. For., Tech. Rep. 5, 41 p., Toronto.

Aldhous, J. R.
1976. Lodgepole pine seed zones with reference to British requirements. *In Pinus contorta* provenance studies, p. 6-39. For. Comm. Res. and Dev. Pap. 114 (Great Britain).

Alexander, R. R., D. Tackle, and W. G. Dahms.
1967. Site indexes for lodgepole pine, with corrections for stand density: methodology. U.S. For. Serv. Res. Pap. RM-29, 18 p. Rocky Mt. For. and Range Exp. Stn., Fort Collins, Colo.

American Forestry Association.
1951. Report on American big trees, part V. Amer. Forests 57(8):22.

Amman, G. D.
1975. Insects affecting lodgepole pine productivity. *In* Management of lodgepole pine ecosystems: symposium proceedings,vol. 1, p. 310-341. Coop. Ext. Serv., Wash. State Univ., Pullman. [Pullman, Wash., Oct. 9-11, 1973].

Anderson, J. H.
1970. A geobotanical study in the Atlin region in northwestern British Columbia and south-central Yukon Territory. Ph.D. thesis, Mich. State Univ., East Lansing. 380 p.

Anderson, N. A., and R. L. Anderson.
1965. The susceptibility of jack pine and lodgepole pine and their hybrids to sweetfern rust and eastern gall rust. U.S. For. Serv. Res. Note LS-56, 4 p. Lake States For. Exp. Stn., St. Paul, Minn.

Argus, G. W.
1966. Botanical investigations in northeastern Saskatchewan: the subarctic Patterson-Hasbala Lakes region. Can. Field-Nat. 80: 119-143.

Armit, D.
1964. Cone habit of lodgepole pine. *In* British Columbia For. Serv. Res. Rev. 1963-1964, p. 56-57. Victoria.

Armit, D.
1968. Seed dispersal study, Verdun Mountain. *In* British Columbia For. Serv. Res. Rev. 1967-1968, p. 32-33. Victoria.

Arno, S. F.
1976. The historical role of fire on the Bitterroot National Forest. USDA For. Serv. Res. Pap. INT-187, 29 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Austin, L.
1929. The Eddy Tree Breeding Station. Madroño 1:203-212.

Axelrod, D. I.
1944. The Alvord Creek flora. *In* Pliocene floras of California and Oregon. Carnegie Inst. Wash. Publ. 553, p 225-262.

Axelrod, D. I., and W. S. Ting.
1960. Late Pliocene floras east of the Sierra Nevada. Univ. Calif. Publ. Geol. Sci. 39:1-118.

Axelrod, D. I., and W. S. Ting.
1961. Early Pleistocene floras from the Chagoopa surface, southern Sierra Nevada. Univ. Calif. Publ. Geol. Sci. 39:119-194.

Baker, H. G.
1972. Seed weight in relation to environmental conditions in California. Ecology 53:997-1,010.

Baker, R. G.
1970. Pollen sequence from Late Quaternary sediments in Yellowstone Park. Science 168:1,449-1,450.

Baker, R. G.
1976. Late Quaternary vegetation history of the Yellowstone Lake Basin, Wyoming. Geol. Surv. Prof. Pap. 729-E, 48 p.

Bannan, M. W.
1964. Tracheid size and anticlinal divisions in the cambium of lodgepole pine. Can. J. Bot. 42:1,105-1,118.

Bannister, M. H.
1965. Variation in the breeding system of *Pinus radiata*. *In* The genetics of colonizing species, H. G. Baker and G. L. Stebbins, eds., p. 353-372. Academic Press, New York.

Baranyay, J. A.
1975. Dwarf mistletoe as a factor in the management of lodgepole pine forests in western Canada. *In* Management of lodgepole pine ecosystems: symposium proceedings, vol. 1, p. 359-376. Coop. Ext. Serv., Wash. State Univ., Pullman. [Pullman, Wash., Oct. 9-11, 1973].

Bates, C. G.
1930. The production, extraction, and germination of lodgepole pine seed. U.S. Dep. Agric., Tech. Bull. 191, 92 p.

Bates, C. G., H. C. Hilton, and T. Krueger.
1929. Experiments in the silvicultural control of natural reproduction of lodgepole pine in the central Rocky Mountains. J. Agric. Res. 38:229-243.

Baumgartner, D. M., ed.
1975. Management of lodgepole pine ecosystems: symposium proceedings, 2 vols., 825 p. Coop. Ext. Serv., Wash. State Univ., Pullman. [Pullman, Wash., Oct. 9-11, 1973].

Beaufait, W. R.
1960. Some effects of high temperatures on the cones and seeds of jack pine. For. Sci. 6:194-199.

Berntsen, C. M.
1967. Relative low temperature tolerance of lodgepole and ponderosa pine seedlings. Ph.D. thesis. Oregon State Univ., Corvallis, 158 p.

Birot, Y.
1978. Variabilité géographique du poids de la graine de *Pinus contorta*. Silvae Genet. 27:32-40.

Black, T. M.
1961. Abnormalities of the reproductive system of *Pinus contorta* Loudon. Ann. Bot., N.S., 25:21-28.

Black, T. M.
1963a. Some features of the timber anatomy of *P. contorta* Loudon and *P. banksiana* Lambert. J. Inst. Wood Sci. 2,11:57-65.

Black, T. M.
1963b. The resin canals of *Pinus contorta* Loudon. Irish For. 20:69-85.

Blackman, T.
1978. Genetics center moves toward objective of tree improvement. For. Ind. 105(1):64-65.

Blankensop, C. M.
1968. The hybrid Christmas tree can be successfully rooted. Calif. Christmas Tree Growers Bull. 63:14-15.

Boe, K. N.
1954. Periodicity of cone crops for five Montana conifers. Proc. Montana Acad. Sci. 14:5-9.

Boe, K. N.
1956. Regeneration and slash disposal in lodgepole pine clear cuttings. Northwest Sci. 30:1-11.

Boivin, B.
1966. Énumération des plantes du Canada. Nat. Can. 93: 253-273.

Bowen, M. R., J. Howarth, and K. A. Longman.
1975. Effects of auxins and other factors on the rooting of *Pinus contorta* Dougl. cuttings. Ann. Bot. 39:647-656.

Bright, R. C.
1966. Pollen and seed stratigraphy of Swan Lake, southeastern Idaho. Tebiwa 9(2), 47 p.

British Columbia Forest Service.
1977. Forest research review, year ended March 1977. 87 p. Victoria.

Brown, I. R.
1970. Premature cone loss in grafted clones of Scots pine. Proc. Symp., Sexual reproduction of forest trees. Vol. 1. IUFRO Sec. 22 Work. Group, 15 p.

Brown, J. K.
1975. Fire cycles and community dynamics in lodgepole pine forests. *In* Management of lodgepole pine ecosystems: symposium proceedings, vol. 1, p. 429-456. Coop. Ext. Serv., Wash. State Univ., Pullman. [Pullman, Wash., Oct. 9-11, 1973].

Buchholz, J. T.
1945. Embryological aspects of hybrid vigor in pines. Science 102:135-142.

Callaham, R. Z., and R. J. Steinhoff.
1966. Pine pollens frozen five years produce seed. U.S. For. Serv. Res. Pap. NC-6:94-101. North Cent. For. Exp. Stn., St. Paul, Minn.

Cameron, H.
1953. Melting point of the bonding material in lodgepole pine and jack pine cones. Can. For. Br., Div. For. Res., Silvic. Leafl. 86, 3 p. Ottawa.

Cannell, M. G. R.
1974. Production of branches and foliage by young trees of *Pinus contorta* and *Picea sitchensis*: provenance differences and their simulation. J. Appl. Ecol. 11:1,091-1,115.

Cannell, M. G. R.
1976a. Shoot apical growth and cataphyll initiation rates in provenances of *Pinus contorta* in Scotland. Can. J. For. Res. 6:539-556.

Cannell, M. G. R.
1976b. Some causes and consequences of differences in height growth and branch frequency on differing provenances of *Pinus contorta*. *In Pinus contorta* provenance studies, p. 43-51. For. Comm. Res. and Dev. Pap. 114 (Great Britain).

Cannell, M. G. R., S. Thompson, and R. Lines.
1976. An analysis of inherent differences in shoot growth within some north temperate conifers. *In* Tree physiology and yield improvement, p. 173-205. Academic Press, London.

Cannell, M. G. R., and S. C. Willett.
1975. Rates and times at which needles are initiated in buds on differing provenances of *Pinus contorta* and *Picea sitchensis* in Scotland. Can. J. For. Res. 5:367-380.

Cannell, M. G. R., and S. C. Willett.
1976. Shoot growth phenology, dry matter distribution and root:shoot ratios of provenances of *Populus trichocarpa*, *Picea sitchensis* and *Pinus contorta* growing in Scotland. Silvae Genet. 25:49-59.

Chamberlain, C. J.
1935. Gymnosperms: structure and evolution. 484 p. Univ. Chicago Press, Chicago.

Clausen, J.
1963. Tree lines and germ plasm—a study in evolutionary limitations. Proc. Natl. Acad. Sci. 50:860-868.

Clausen, J.
1965. Population studies of alpine and subalpine races of conifers and willows in the California High Sierra Nevada. Evolution 19:56-68.

Clausen, J.
1968. Clusters of tree species on both sides of the Pacific. Annu. Rep. Dir. Dep. Plant Biol., Carnegie Inst., 1966-1967:234-243.

Clements, F. E.
1910. The life history of lodgepole burn forests. U.S. Dep. Agric., For Serv., Bull. 79, 56 p. Washington, D.C.

Cochran P. H.
1972. Tolerance of lodgepole and ponderosa pine seeds and seedlings to high water tables. Northwest Sci. 46:322-331.

Cochran, P. H.
1973. Natural regeneration of lodgepole pine in south-central Oregon. USDA For. Serv. Res. Note PNW-204, 18 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Cochran, P. H.
1975. Soil temperatures and natural forest regeneration in south-central Oregon. *In* Forest soils and forest land management. p. 37-52. B. Bernier and C. H. Winget, eds. Laval Univ. Press, Quebec.

Cochran, P. H., and C. M. Berntsen.
1973. Tolerance of lodgepole and ponderosa pine seedlings to low night temperatures. For. Sci. 19:272-280.

Cody, W. J.
1963. A contribution to the knowledge of the flora of south-western Mackenzie District N.W.T. Can. Field-Nat. 77: 108-123.

Copes, D. L.
1975. Graft incompatibility in *Pinus contorta*. USDA For. Serv. Res. Note PNW-260, 9 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Cremer, K. W.
1971. Speeds of falling and dispersal of seed of *Pinus radiata* and *P. contorta*. Austral. For Res. 5:29-32.

Critchfield, W. B.
1957. Geographic variation in *Pinus contorta*. Maria Moors Cabot Found. Publ. 3, 118 p. Harvard Univ., Cambridge, Mass.

Critchfield, W. B.
1963. Hybridization of the southern pines in California. South. Forest Tree Improv. Comm. Publ. 22:40-48.

Critchfield, W. B.
1965. A new hybrid Christmas tree. South. Lumberman 211(2,632):132-133.

Critchfield, W. B., and E. L. Little, Jr.
1966. Geographic distribution of the pines of the world. U.S. Dep. Agric. Misc. Publ. 991, 97 p. Washington, D.C.

Crossley, D. I.
1955a. The production and dispersal of lodgepole pine seed. Can. For. Br., For. Res. Div. Tech. Note 25, 12 p.

Crossley, D. I.
1955b. Viability of the seed of lodgepole pine after 20 years in artificial storage. For. Chron. 31:250-253.

Crossley, D. I.
1956a. Fruiting habits of lodgepole pine. Can. For. Br., For. Res. Div. Tech. Note 35, 32 p.

Crossley, D. I.
1956b. Effect of crown cover and slash density on the release of seed from slash-borne lodgepole pine cones. Can. For. Br., For. Res. Div. Tech. Note 41, 51 p.

Crossley, D. I.
1976. The ingress of regeneration following harvesting and scarification of lodgepole pine stands. For. Chron. 52:17-21.

Cumming, W. C., and F. I. Righter.
1948. Methods used to control pollination of pines in the Sierra Nevada of California. U.S. Dep. Agric. Circ. 792, 18 p. Washington, D.C.

Cunningham, A., and Q. Roberts.
1970. A provenance trial of *Pinus contorta* at 4,800 ft in the Kaweka Range. N. Z. J. For. 15:79-87.

Dahms, W. G.
1975. Gross yield of central Oregon lodgepole pine. *In* Management of lodgepole pine ecosystems: symposium proceedings, vol. 1, p. 208-232, Coop. Ext. Serv., Wash. State Univ., Pullman. [Pullman, Wash., Oct. 9-11, 1973].

Dahms, W. G., and J. W. Barrett.
1975. Seed production of central Oregon ponderosa and lodgepole pines. USDA For. Serv. Res. Pap. PNW-191, 13 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Dancik, B. P.
1979. Forest genetics studies at the University of Alberta. 17th Meet. Can. Tree Improv. Assoc., Members' Rep., 5 p.

Dietrichson, J.
1976. Norwegian experiments with *Pinus contorta*. *In Pinus contorta* provenance studies, p. 74. For. Comm. Res. and Dev. Pap. 114 (Great Britain).

Dietrichson, J.
1970. [Geographic variation in *Pinus contorta* Dougl. A study aiming at the use of the species in Norway.] Medd. Norske Skogforsøksv. No. 102, 28:114-140. [In Norw., Engl. summ.].

Drouin, J. A., C. R. Sullivan, and S. G. Smith.
1963. Occurrence of *Pissodes terminalis* Hopp. (Coleoptera: Curculionidae) in Canada: life history, behaviour, and cytogenetic identification. Can. Entomol. 95:70-76.

Duffield, J. W.
1952. Relationships and species hybridization in the genus *Pinus*. Z. Forstgenet. Forstplanzenzücht. [Silvae Genet.] 1:93-100.

Duffield, J. W.
1953. Pine pollen collection dates—annual and geographic variation. U.S. For. Serv., Calif. For. and Range Exp. Stn., For. Res. Note 85, 9 p. Berkeley, Calif.

Dykstra, G. F.
1974. Drought resistance of lodgepole pine seedlings in relation to provenance and tree water potential. British Columbia For. Serv. Res. Notes 62, 11 p. Victoria.

Edwards, M. V.
1954-1955. A summary of information on *Pinus contorta* with special reference to its use in Europe. For. Abstr. 15:389-396, 16:3-13.

Ehrenberg, C., Å. Gustafsson, C. Plym Forshell, and M. Simak.
1955. Seed quality and the principles of forest genetics. Hereditas 41:291-366.

Ehrenberg, C. E.
1960. Studies on the longevity of stored pine pollen (*Pinus silvestris* L. and *Pinus contorta* var. *Murrayana* Engelm.). Medd. Stat. Skogsforskningsinst. 49(7), 31 p.

Ekberg, I., G. Eriksson, and A. Jonsson.
1972. Meiosis in pollen mother cells of *Pinus contorta*. Hereditas 71:313-324.

Elliott, P. F.
1974. Evolutionary responses of plants to seed-eaters: pine squirrel predation on lodgepole pine. Evolution 28:221-231.

Faulkner, R.
1974. An outline of the British tree breeding programme. *In* Forest tree breeding in the world, p. 1-8. Gov. For. Exp. Stn., Japan.

Feilberg, L.
1964. *Pinus contorta* (lodgepole pine), its provenances and breeding. Dansk Skovforen. Tidskr. 49:267-296. (Engl. transl. *In* For. Comm. Lib. Rev. 1:10-21, 1965 (Great Britain)).

Forbes, A. C.
1928. *Pinus contorta* or *P. murrayana*. Gard. Chron. 83: 232-234.

Forestry Commission (Great Britain)
1967. Report on forest research for the year ended March 1967. 194 p. London.

Forestry Commission (Great Britain).
1968. Report on forest research for the year ended March 1968. 193 p. London.

Forestry Commission (Great Britain).
1969. Report on forest research for the year ended March 1969. 203 p. London.

Forestry Commission (Great Britain).
1970. Report on Forest Research, 1970. 240 p. London.

Forestry Commission (Great Britain).
1971. Report on Forest Research, 1971. 171 p. London.

Forestry Commission (Great Britain).
1972. Report on Forest Research, 1972. 193 p. London.

Forestry Commission (Great Britain).
1975. Report on Forest Research, 1975. 104 p. London.

Forestry Commission (Great Britain).
1976. Report on forest research for the year ended March 1976. 101 p. London.

Forestry Commission (Great Britain).
1977. Report on forest research for the year ended March 1977. 90 p. London.

Forrest, G. I.
1977. Geographical variation in the monoterpenes of the resin of *Pinus contorta*. *In* EEC Symposium on forest tree biochemistry, p. 55-71. Comm. Eur. Communities, Brussels. [Brussels, Belgium, Jan. 25-27, 1977].

Fosberg, F. P.
1959. *Pinus contorta* and its variations. Baileya 7:7-10.

Foundation for Forest Tree Breeding.
1977. Foundation for Forest Tree Breeding in Finland 1977 [Annu. Rep.] 31 p. Helsinki.

Franklin, E. C.
1970. Survey of mutant forms and inbreeding depression in species of the family Pinaceae. USDA For. Serv. Res. Pap. SE-61, 21 p. Southeast. For. Exp. Stn., Asheville, N.C.

Franklin, E. C., and R. Z. Callaham.
1970. Multinodality, branching, and forking in lodgepole pine (*Pinus contorta* var. *murrayana* Engelm.). Silvae Genet. 19:180-184.

Franklin, J. F., and C. T. Dyrness.
1973. Natural vegetation of Oregon and Washington. USDA Forest Serv. Gen. Tech. Rep. PNW-8, 417 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Garman, E. H.
1973. The trees and shrubs of British Columbia. British Columbia Prov. Mus. Handb. 31, 5th ed. 131 p. Victoria.

Gorman, M. W.
1896. Economic botany of southeastern Alaska. Pittonia 3:64-85.

Haasis, F. W., and A. C. Thrupp.
1931. Temperature relations of lodgepole-pine seed germination. Ecology 12:728-744.

Hagman, M.
1964. Incompatibility in *Pinus*. Hereditas 52:245 (Abstr.).

Hagman, M.
1967. Genetic mechanisms affecting inbreeding and outbreeding in forest trees; their significance for microevolution of forest tree species. Int. Union For. Res. Organ. 14th Congr. 3:346-365.

Hagner, M.
1970. A genecological investigation of the annual rhythm of *Pinus contorta* Dougl. and a comparison with *Pinus silvestris* L. Stud. For. Suecica 81, 26 p. Roy. Coll. For., Stockholm.

Hagner, S.
1971. [Cultivation of *Pinus contorta* in northern Sweden.] Sver. Skogsvårdsförb. Tidskr. 69:219-246. [In Swed., Engl. summ.].

Hagner, S., and S. Fahlroth.
1974. [On the prospects of cultivating *Pinus contorta* in North Sweden.] Sver. Skogsvårdsförb. Tidskr. 72:477-528. 72:477-528. [In Swed., Engl. summ.].

Hahl, J.
1978. [Results from an eight-year old provenance trial of lodgepole pine (*Pinus contorta* Dougl.)] Foundation for Forest Tree Breeding in Finland, Inform. 4, 7 p. [In Finn., Engl. summ.].

Hakkila, P., and A. Panhelainen.
1970. On the wood properties of *Pinus contorta* in Finland. Comm. Inst. For. Fenn. 73.1, 43 p. Helsinki.

Hanan, A. M. S.
1963. "Bolander's pine?" Irish For. 20:3-6.

Hansen, H. P.
1967. Chronology of postglacial pollen profiles in the Pacific Northwest (U.S.A.). Rev. Palaeobot. Palynol. 4:103-105.

Harris, J. M.
1971. Physical properties, resin content, and tracheid length of lodgepole pine grown in New Zealand. N.Z. J. For. Sci. 3:91-109.

Hawksworth, F. G.
1975. Dwarf mistletoe and its role in lodgepole pine ecosystems. *In* Management of lodgepole pine ecosystems: symposium proceedings, vol. 1, p. 342-358. Coop. Ext. Serv., Wash. State Univ., Pullman. [Pullman, Wash., Oct. 9-11, 1973].

Hawksworth, F. G., and D. Wiens.
1972. Biology and classification of dwarf mistletoes *(Arceuthobium)*. U.S. Dep. Agric., Agric. Handb. 401, 234 p.

Hayes, A. J.
1975. The mode of infection of lodgepole pine by *Crumenula soraria* Karst. and the susceptibility of different provenances to attack. Forestry 48:99-113.

Hedlin, A. F.
1974. Cone and seed insects of British Columbia. Can. For. Serv., Pac. For. Res. Cent. Rep. BC-X-90, 63 p. Victoria.

Heiser, C. B., Jr.
1959. Natural hybridization and introgression with special reference to *Helianthus*. Recent Adv Bot. 1:874-877.

Henderson, J., and J. A. Petty.
1972. A comparison of wood properties of coastal and interior provenances of lodgepole pine *Pinus contorta* Dougl. ex Loud. Forestry 45:49-57.

Heusser, C. J.
1965. A Pleistocene phytogeographical sketch of the Pacific Northwest and Alaska. *In* The Quaternary of the United States, p. 469-483. Princeton Univ. Press, Princeton, N.J.

Heusser, C. J.
1969. Late-Pleistocene coniferous forests of the northern Rocky Mountains. *In* Coniferous forests of the northern Rocky Mountains, p. 1-21. Univ. Mont. Found., Missoula.

Heusser, C.
1973. Environmental sequence following the Fraser advance of the Juan de Fuca lobe, Washington. Quat. Res. 3:284-306.

Ho, R. H., and J. N. Owens.
1973. Microstrobili of lodgepole pine. Can. J. For. Res. 3:453-456.

Ho, R. H., and J. N. Owens.
1974. Microsporogenesis and pollen formation in lodgepole pine. Can. J. Bot. 52:1,669-1,674.

Ho, R. H., and O. Sziklai.
1971. Germination and development of lodgepole pine pollen *in vitro*. Can. J. For. Res. 1:12-19.

Hocking, D.
1972. Effects of stratification of Alberta white spruce and lodgepole pine seeds on emergence in operational seedbeds. Can. For. Serv., Bi-month. Res. Notes 28:26-27.

Hoffman, G. R., and R. R. Alexander.
1976. Forest vegetation of the Bighorn Mountains: a habitat type classification. USDA For. Serv. Res. Pap. RM-170, 38 p. Rocky Mt. For. and Range Exp. Stn., Fort Collins, Colo.

Holst, M. J., J. A. Santon, and C. W. Yeatman.
1956. Greenhouse grafting of spruce and hard pine at the Petawawa Forest Experiment Station, Chalk River, Ontario. Can. For. Br., For. Res. Div., Tech. Note 33, 24 p.

Hopkins, D. M.
1967. The Cenozoic history of Beringia—a synthesis. *In* The Bering land bridge, p. 451-484. Stanford Univ. Press, Stanford, Calif.

Hopkins, D. M., J. V. Matthews, J. A. Wolfe, and M. L. Silberman.
1971. A Pliocene flora and insect fauna from the Bering Strait region. Palaeogeogr., Palaeoclimatol., Palaeoecol. 9:211-231.

Horton, K. W.
1953. Causes of variation in the stocking of lodgepole pine regeneration following fire. Can. For. Br., For. Res. Div., Silvic. Leafl. 95, 5 p.

Horton, K. W.
1956. The ecology of lodgepole pine in Alberta and its role in forest succession. Can. For. Br., For. Res. Div. Tech. Note 45, 29 p.

Howe, G. E.
1973. The forest genetics program for the Northern Region. USDA, For. Serv., North. Reg., Missoula, Mont. 78 p.

Howell, J. T.
1946. Base camp botany, 1946. 17 p. Sierra Club, San Francisco, Calif.

Hultén, E.
1937. Outline of the history of Arctic and boreal biota during the Quaternary Period. 168 p. Bokförlags Aktiebolaget Thule, Stockholm.

Iktüeren, S.
1973. [Studies on the propagation of *Pinus contorta* Douglas by stem cuttings.] Ormanc. Araşt. Enst. Yayinl., Muhtelif Yayinl. Ser. No. 32, 242 p. Ankara. [In Turk., Eng. summ.].

Illingworth, K.
1970. Regional variation in lodgepole pine cone habit in Canada. *In* British Columbia Forest Service, For. Res. Rev. 1969-1970, p. 105-106.

Illingworth, K.
1971. Variation in *Pinus contorta* with particular reference to British Columbia. *In* British Columbia Forest Service, For. Res. Rev. 1970-1971, p. 34-36.

Illingworth, K.
1973. Variation in the susceptibility of lodgepole pine provenances to *Sirococcus* shoot blight. Can. J. For. Res. 3:585-589.

Illingworth, K.
1975. Lodgepole pine provenance research and breeding in British Columbia. *In* Management of lodgepole pine ecosystems: symposium proceedings, vol. 1, p. 47-57. Coop. Ext. Serv., Wash. State Univ., Pullman. [Pullman, Wash., Oct. 9-11, 1973].

Illingworth, K.
1976a. Inter- and intra-provenance variation in heights of three-year-old *Pinus contorta* Dougl. *In Pinus contorta* provenance studies, p. 90-103. For. Comm. Res. and Develop. Pap. 114 (Great Britain).

Illingworth, K.
1976b. Natural variation within lodgepole pine in British Columbia. *In Pinus contorta* provenance studies, p. 40-42. For. Comm. Res. and Dev. Pap. 114 (Great Britain).

Illingworth, K.
1976c. Provenance research by the British Columbia Forest Service, 1973-75. Proc. 15th Meet. Can. Tree Improv. Assoc., part I:173-176.

Industrial Forestry Association.
1975. IFA tree improvement newsletter 27, 9 p. Olympia, Wash.

Industrial Forestry Association.
1977. IFA tree improvement newsletter 31, 26 p. Olympia, Wash.

Industrial Forestry Association.
1978. IFA tree improvement newsletter 34, 32 p. Olympia, Wash.

Jameson, J. S.
1961. Observations on factors influencing jack pine reproduction in Saskatchewan. Can. Dep. For., For. Res. Div. Tech. Note 97, 24 p.

Jeffers, J. N. R., and T. M. Black.
1963. An analysis of variability in *Pinus contorta*. Forestry 36:199-218.

Jenny, H., R. J. Arkley, and A. M. Schultz.
1969. The pygmy forest-podsol ecosystem and its dune associates of the Mendocino coast. Madroño 20:60-74.

Johnsson, L. C., and W. B. Critchfield.
1979. The production of functional pollen and ovules by pine seedlings less than 1 year old. For. Sci. 24:467-468.

Johnson, H.
1975. Observations on induced polyploidy in some conifers. Silvae Genet. 24:62-68.

Johnstone, W. D.
1976. Ingress of lodgepole pine and white spruce regeneration following logging and scarification in west-central Alberta. Can. For. Serv., North. For. Res. Cent., Inf. Rep. NOR-X-170, 12 p. Edmonton.

Kaufmann, M. R., and A. N. Eckard.
1977. Water potential and temperature effects on germination of Engelmann spruce and lodgepole pine seeds. For. Sci. 23:27-33.

Keen, F. P.
1952. Insect enemies of western forests. U.S. Dep. Agric. Misc. Pub. 273, 280 p.

Keen, F. P.
1958. Cone and seed insects of western forest trees. U.S. Dep. Agric. Tech. Bull. 1169, 168 p.

Kienholz, R.
1931. Effect of environmental factors on the wood structure of lodgepole pine, *Pinus contorta* Loudon. Ecology 12:354-379.

Knowlton, F. H.
1899. Fossil flora of the Yellowstone National Park. *In* Geology of the Yellowstone National Park, part II, p. 651-882. U.S. Geol. Surv. Monogr. 32.

Koerber, T. W., and G. R. Struble.
1971. Lodgepole needle miner. USDA For. Serv., For. Pest Leafl. 22 (rev.), 8 p.

Krebill, R. G.
1968. *Cronartium comandrae* in the Rocky Mountain states. USDA For. Serv. Res. Pap. INT-50, 28 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Kriek, W.
1973. [*Pinus contorta* provenance trials in the Netherlands.] Ned. Bosb. Tijdschr. 45:141-153. [In Dutch, Engl. summ.]

Kriek, W.
1976. *Pinus contorta* provenances in the Netherlands. *In Pinus contorta* provenance studies, p. 75-80. For. Comm. Res. and Dev. Pap. 114 (Great Britain).

Kruckeberg, A. R.
1967. Ecotypic response to ultramafic soils by some plant species of northwestern United States. Brittonia 19:133-151.

Kuijt, J.
1963. Distribution of dwarf mistletoes and their fungus hyperparasites in western Canada. Nat. Mus. Can. Bull. 186, Contr. Bot., 1960-61:134-148.

Lang, K. J., P. Neumann, and P. Schütt.
1971. Der Einfluss von Samenherkunft und Düngung auf die SO_2-Härte von *Pinus contorta*-Sämlingen. Flora (Jena) 160:1-9.

Larsen, F. E., and R. W. Dingle.
1969. Vegetative propagation of lodgepole pine (*Pinus contorta* Dougl.) from needle fascicles. For. Sci. 15:64-65.

Lavender, D. P.
1978. Seed collection, handling, and damage. *In* Regenerating Oregon's forests, p. 53-62. B. D. Cleary, R. D. Greaves, and R. K. Hermann, compilers and eds. Oreg. State Univ. Ext. Serv., Corvallis, Oreg.

Lemke, R. W., W. M. Laird, M. J. Tipton, and R. M. Lindvall.
1965. Quaternary geology of northern Great Plains. *In* The Quaternary of the United States, p. 15-27. Princeton Univ. Press, Princeton, N.J.

Lichti-Federovich, S.
1970. The pollen stratigraphy of a dated section of Late Pleistocene lake sediment from central Alberta. Can. J. Earth Sci. 7:938-945.

Lichti-Federovich, S.
1972. Pollen stratigraphy of a sediment core from Alpen Siding Lake, Alberta. Geol. Surv. Can. Pap. 72-1(B):113-115.

Lichti-Federovich, S.
1974. Palynology of two sections of Late Quaternary sediments from the Porcupine River, Yukon Territory. Can. Geol. Surv. Pap. 74-23, 6 p.

Lindgren, D., P. Krutzch, J. Twetman, and C. L. Kiellander.
1976. Survival and early growth of *Pinus contorta* provenances in northern Sweden. Dep. For. Gen. Res. Note 20, 42 p. Roy. Coll. For., Stockholm, Sweden.

Lines, R.
1957. *Pinus contorta* in Ireland, 1955. Forestry 30:137-150.

Lines, R.
1966. Choosing the right provenance of lodgepole pine (*Pinus contorta*). Scot. For. 20:90-103.

Lines R.
1976a. Notes on selected experiments seen on tour 10-13/9/74. *In Pinus contorta* provenance studies, p. 110-124. For. Comm. Res. and Dev. Pap. 114 (Great Britain).

Lines, R., ed.
1976b. *Pinus contorta* provenance studies. For. Comm. Res. and Dev. Pap. 114 (Great Britain). 128 p.

Lines, R.
1976c. The development of forestry in Scotland in relation to the use of *Pinus contorta*. *In Pinus contorta* provenance studies. p. 2-5. For. Comm. Res. and Dev. Pap. 114 (Great Britain).

Lines, R.
1977. Variation in flowering in forest trees. Quart. J. For. 71:7-14.

Lines, R., and T. C. Booth.
1972. Investigation of basal sweep of lodgepole and shore pines in Great Britain. Forestry 45:59-66.

Linsley, E. G.
1962. The Cerambycidae of North America part II. Taxonomy and classification of the Parandrinae, Prioninae, Spondylinae, and Aseminae. Univ. Calif. Publ. Entomol. 19, 102 p.

Little, E. L., Jr.
1953. Checklist of native and naturalized trees of the United States (including Alaska). U.S. Dep. Agric., Agric. Handb. 41, 472 p.

Little, E. L., Jr.
1971. Atlas of United States trees, vol. 1. Conifers and important hardwoods. U.S. Dep. Agric., Misc. Publ. 1146, 9 p. (313 maps).

Little, E. L., Jr., and W. B. Critchfield.
1969. Subdivisions of the genus *Pinus* (pines). U.S. Dep. Agric., Misc. Publ. 1144, 51 p.

Løfting, E. C. L.
1966. [Provenance experiments with *Pinus contorta* (Loud.).] Forst. Forsøgsvaes. Danm. 30:53-95. [In Danish, Engl. summ.].

Longman, K. A.
1961. Factors affecting flower initiation in certain conifers. Proc. Linn. Soc. London 172:124-127.

Lopushinsky, W.
1975. Water relations and photosynthesis in lodgepole pine. *In* Management of lodgepole pine ecosystems: symposium proceedings, vol. 1, p. 135-153. Coop. Ext. Serv., Wash. State Univ., Pullman. [Pullman, Wash., Oct. 9-11, 1973].

Lotan, J. E.
1964. Initial germination and survival of lodgepole pine on prepared seedbeds. USDA For. Serv. Res. Note INT-29, 8 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Lotan, J. E.
1967a. Cone serotiny of lodgepole pine near West Yellowstone, Montana. For. Sci. 13:55-59.

Lotan, J. E.
1967b. Early performance of *Pinus contorta* × *banksiana* hybrids. USDA For. Serv. Res. Note INT-57, 8 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Lotan, J. E.
1968. Cone serotiny of lodgepole pine near Island Park, Idaho. USDA For. Serv. Res. Pap. INT-52, 6 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Lotan, J. E.
1970. Cone serotiny in *Pinus contorta*. Ph.D. thesis, Univ. Mich., Ann Arbor. 94 p.

Lotan, J. E.
1975a. The role of cone serotiny in lodgepole pine forests. *In* Management of lodgepole pine ecosystems: symposium proceedings, vol. 1, p. 471-495. Coop. Ext. Serv., Wash. State Univ., Pullman. [Pullman, Wash., Oct. 9-11, 1973].

Lotan, J. E.
1975b. Regeneration of lodgepole pine forests in the northern Rocky Mountains. *In* Management of lodgepole pine ecosystems: symposium proceedings, vol. 2, p. 516-535. Coop. Ext. Serv., Wash. State Univ., Pullman. [Pullman, Wash., Oct. 9-11, 1973].

Lotan, J. E.
1976. Cone serotiny-fire relationships in lodgepole pine. Proc. Mont. Tall Timbers Fire Ecol. Conf. and Fire and Land Manag. Symp. 14:267-278. Tall Timbers Res. Stn., Tallahassee, Fla.

Lotan, J. E., and N. M. Joye, Jr.
1970. Some variation of terpenes in Montana lodgepole pine. USDA For. Serv. Res. Note INT-120, 4 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Löve, D.
1959. The postglacial development of the flora of Manitoba: a discussion. Can. J. Bot. 37:547-585.

Macaulay Institute.
1969. Root and moisture studies. Rep. Macaulay Inst. Soil Res. 1968/69:15.

Mack, R. N.
1971. Pollen size variation in some western North American pines as related to fossil pollen identification. Northwest Sci. 45:257-267.

Mack, R. N., V. M. Bryant, Jr., and R. Fryxell.
1976. Pollen sequence from the Columbia Basin, Washington: reappraisal of of postglacial vegetation. Amer. Midl. Nat. 95:390-397.

Martin, H. A., and G. L. Rouse.
1966. Palynology of late Tertiary sediments from Queen Charlotte Islands, British Columbia. Can. J. Bot. 44:171-208.

Maschning, E.
1971. Die Variation der Kotyledonenzahl bei einigen *Pinus contorta*-Herkünften. Silvae Genet. 20:10-14.

Mason, D. T.
1915. The life history of lodgepole pine in the Rocky Mountains. U.S. Dep. Agric. Bull. 154, 35 p.

Mason, R. R., and T. C. Tigner.
1972. Forest-site relationships within an outbreak of lodgepole needle miner in Central Oregon. USDA For. Serv. Res. Pap. PNW-146, 18 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Mathewes, R. W.
1973. A palynological study of postglacial vegetation changes in the University Research Forest, southwestern British Columbia. Can. J. Bot. 51: 2,085-2,103.

Matthews, J. V., Jr.
1970. Quaternary environmental history of interior Alaska: pollen samples from organic colluvium and peats. Arct. and Alp. Res. 2:241-251.

McLeod, J. M.
1961. *Evagora canusella* Free. on jack-pine in Quebec. Can. Dep. For., For. Biol. Div. Bi-month. Progr. Rep. 17:1-2.

McMillan, C.
1964. Survival of transplanted *Cupressus* and *Pinus* after thirteen years in Mendocino County, California. Madroño 17:250-253.

Miller, J. T.
1969. An approach to the improvement of *Pinus contorta* in New Zealand. 2nd World Consult. For. Tree Breed., Washington, D.C. FO-FTB-69-9/12. 9 p.

Mills, E. A.
1915. The Rocky Mountain wonderland. 363 p. Houghton Mifflin Co., Boston and New York.

Minore, D.
1968. Effects of artificial flooding on seedling survival and growth of six Northwestern tree species. USDA For. Serv. Res. Note PNW-92, 11 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Minore, D.
1970. Seedling growth of eight northwestern tree species over three water tables. USDA For. Serv. Res. Note PNW-115, 8 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Mirov, N. T.
1956. Composition of turpentine of lodgepole × jack pine hybrids. Can. J. Bot. 34:443-457.

Mirov, N. T.
1961. Composition of gum turpentine of pines. U.S. Dep. Agric. Tech. Bull. 1239, 158 p.

Moir, W. H.
1969. The lodgepole pine zone in Colorado. Amer. Midl. Nat. 81:87-98.

Mooney, O. V.
1957. *Pinus contorta* in Irish forestry. Irish For. 14:77-89.

Morden, G., and J. Ross.
1976. Ponderosa and lodgepole pine rooting trials. Tree Plant. Notes 27(4):10-13.

Moss, A.
1971. An investigation of basal sweep of lodgepole and shore pines in Great Britain. Forestry 44:43-65.

Moss, E. H.
1949. Natural pine hybrids in Alberta. Can. J. Res., Sec. C, Bot. Sci. 27:218-229.

Mott, R. J.
1973. Palynological studies in central Saskatchewan. Geol. Surv. Can. Pap. 72-49, 18 p.

Mowat, E. L.
1960. No serotinous cones on central Oregon lodgepole pine. J. For. 58:118-119.

Munz, P. A.
1959. A California flora. 1,681 p. Univ. Calif. Press, Berkeley.

Newsome, R. D., and R. L. Dix.
1968. The forests of the Cypress Hills, Alberta and Saskatchewan, Canada. Amer. Midl. Nat. 80:118-185.

North, M. E. A.
1976. A plant geography of Alberta. 147 p. Dep. Geogr., Univ. Alberta, Edmonton.

O'Driscoll, J.
1972. Tree improvement. *In* Forest Research Review 1964-70, p. 13-44. For. and Wildl. Serv., Dep. Lands, Ireland.

Owens, J. N., and M. Molder.
1975. Development of long-shoot terminal buds of *Pinus contorta* ssp. *contorta*. *In* Management of lodgepole pine ecosystems: symposium proceedings, p. 86-104. Coop. Ext. Serv., Wash. State Univ., Pullman. [Pullman, Wash., Oct. 9-11, 1973].

Pardo, R.
1978. National register of big trees. Amer. Forests 84(4):17-47.

Pauly, G., and E. von Rudloff.
1971. Chemosystematic studies in the genus *Pinus:* the leaf oil of *Pinus contorta* var. *latifolia*. Can. J. Bot. 49:1,201-1,210.

Pavlick, L. E.
1971. Variation in volatile oil content of gum oleoresins of *Pinus contorta*, Doug. ex Loud. on Vancouver Island. B.S. thesis. Univ. of Victoria, Victoria.

Perry, D. A., and J. E. Lotan.
1977. Opening temperatures in serotinous cones of lodgepole pine. USDA For. Serv. Res. Note INT-228, 6 p. Intermt. For. and Range Exp. Stn., Odgen, Utah.

Pfister, R. D., and R. Daubenmire.
1975. Ecology of lodgepole pine, *Pinus contorta* Dougl. *In* Management of lodgepole pine ecosystems: symposium proceedings. vol. 1, p. 27-46. Coop. Ext. Serv., Wash. State Univ., Pullman. [Pullman, Wash., Oct. 9-11, 1973].

Pfister, R. D., B. L. Kovalchik, S. F. Arno, and R. C. Presby.
1977. Forest habitat types of Montana. USDA For. Serv. Gen. Tech. Rep. INT-34, 174 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Pharis, R. P., R. L. Wample, and A. Kamienska.
1975. Growth, development, and sexual differentiation in *Pinus*, with emphasis on the role of the plant hormone, gibberellin. *In* Management of lodgepole pine ecosystems: symposium proceedings, vol. 1, p. 106-134. Coop. Ext. Serv., Wash. State Univ., Pullman. [Pullman, Wash., Oct. 9-11, 1973].

Pollack, J. C., and B. P. Dancik.
1979. Atypical needle fascicles in *Pinus contorta*. Can. J. For. Res. 9:538-541.

Porsild, A. E.
1951. Botany of southeastern Yukon adjacent to the Canol Road. Nat. Mus. Can. Bull. 121, 400 p. Ottawa.

Rafn, J.
1915. The testing of forest seeds during 25 years, 1887-1912. 91 p. Langkjaers bogtrykkeri. Copenhagen.

Rampton, V.
1971. Late Quaternary vegetational and climatic history of the Snag-Klutlan area, southwestern Yukon Territory, Canada. Geol. Soc. Amer. Bull. 82:959-978.

Raup, H. M.
1942. Additions to a catalogue of the vascular plants of the Peace and Upper Liard River regions. J. Arnold Arbor. 23:1-28.

Reeves, B. O. K.
1973. The nature and age of the contact between the Laurentide and Cordilleran ice sheets in the western interior of North America. Arct. and Alp. Res. 5:1-16.

Rehfeldt, G. E., and J. E. Lotan.
1970. *Pinus contorta* × *banksiana* hybrids tested in northern Rocky Mountains. USDA For. Serv. Res. Note INT-126, 7 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Righter, F. I.
1939. Early flower production among the pines. J. For. 37:935-938.

Righter, F. I., and P. Stockwell.
1949. The fertile species hybrid, *Pinus murraybanksiana*. Madroño 10:65-69.

Ritchie, J. C.
1976. The late-Quaternary vegetational history of the western interior of Canada. Can. J. Bot. 54:1,793-1,818.

Robak, H.
1976. [Damage registered after winter 1971/72 in field experiments with conifers on firm land in West Norway.] Medd. Norsk Inst. Skogforsk. 32.12, p. 408-455. [In Norw., Engl. summ.].

Roberts, J., and P. F. Wareing.
1975. A study of the growth of four provenances of *Pinus contorta* Dougl. Ann. Bot. 39:93-99.

Roche, L.
1962. Variation in lodgepole pine and its role in the genetic improvement of coastal forms. 102 p. M.F. thesis. Univ. British Columbia, Vancouver.

Roche, L.
1963. The shore variety of *Pinus contorta*. Baileya 11:11-14.

Roche, L.
1966. Variation in lodgepole pine with reference to provenances planted in Great Britain and Ireland. Forestry 39:30-39.

Rudolph, T. D., and H. Nienstaedt.
1962. Polygenic inheritance of resistance to winter injury in jack pine-lodgepole pine hybrids. J. For. 60:138-139.

Rudolph, T. D., R. E. Schoenike, and T. Schantz-Hansen.
1959. Results of one-parent progeny tests relating to the inheritance of open and closed cones in jack pine. Minn. For. Notes 78, 2 p. Univ. Minn., St. Paul.

Rundel, P. W., D. J. Parsons, and D. T. Gordon.
1977. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. *In* Terrestrial vegetation of California. p. 559-599. M. G. Barbour and J. Major, eds. John Wiley and Sons, New York and London.

Salman, K. A.
1935. The effects of attack by *Pissodes terminalis* Hopping on lodgepole pine in California. J. Econ. Entomol. 28:496-497.

Sargent, C. S.
1897. The silva of North America. Vol. 11, Coniferae *(Pinus)*. 163 p. Houghton Mifflin, Boston.

Sarvas, R.
1962. Investigations on the flowering and seed crop of *Pinus silvestris*. Comm. Inst. Forest. Fenn. 53.4, 198 p. Helsinki, Finland.

Savill, P. S.
1976. Lodgepole pine provenance trials in northern Ireland. *In Pinus contorta* provenance studies, p. 88-97. For. Comm. Res. and Dev. Pap. 114 (Great Britain).

Saylor, L. C.
1972. Karyotype analysis of the genus *Pinus*—Subgenus *Pinus*. Silvae Genet. 21:155-163.

Saylor, L. C.
1964. Karotype analysis of *Pinus*—Group *Lariciones*. Silvae Genet. 13:165-170.

Saylor, L. C., and R. L. Koenig.
1967. The slash × sand pine hybrid. Silvae Genet. 16:134-138.

Saylor, L. C., and B. W. Smith.
1966. Meiotic irregularity in species and interspecific hybrids of *Pinus*. Amer. J. Bot. 53:453-468.

Schoenike, R. E.
1962. Natural variation in jack pine (*Pinus banksiana* Lambert). Ph.D. thesis, Univ. Minn., St. Paul. 233 p.

Schoenike, R. E., T. D. Rudolph, and T. Schantz-Hansen.
1959. Cone characteristics in a jack pine seed source plantation. Minn. For. Notes 76, 2 p. Univ. Minn., St. Paul.

Schütt, P.
1958. Schwankungen im Zellulose und Ligningehalt bei einigen in Westdeutschland angebauten *Pinus contorta*-Herkünften. Silvae Genet. 7:65-69.

Scobie, W. R.
1971. Multinodalness and its relation to height growth in juvenile lodgepole pine. M.S. thesis. Wash. State Univ., Pullman. 64 p.

Scotter, G. W.
1974. Distribution of pine (*Pinus* spp.) in the South Nahanni and Flat Rivers region, Northwest Territories. Can. J. For. Res. 4:555-557.

Shrimpton, D. M.
1972. Variation in the extractives from lodgepole pine, sapwood and heartwood. Can. For. Serv., Inf. Rep. NOR-X-18, 22 p. Edmonton.

Siggins, H. W.
1933. Distribution and rate of fall of conifer seeds. J. Agric. Res. 47:119-128.

Smith, C. C.
1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. Ecol. Monogr. 38:31-63.

Smith, C. C.
1970. The coevolution of pine squirrels *(Tamiasciurus)* and conifers. Ecol. Monogr. 40:349-371.

Smith, R. B.
1974. Infection and development of dwarf mistletoes on plantation-grown trees in British Columbia. Can. For. Serv., Pac. For. Res. Cent. Rep. BC-X-97, 21 p. Victoria.

Smith, R. H.
1964. The monoterpenes of lodgepole pine oleoresin. Phytochemistry 3:259-262.

Smith, R. H.
1967. Variations in the monoterpene composition of the wood resin of Jeffrey, Washoe, Coulter and lodgepole pines. For. Sci. 13:246-252.

Smithers, L. A.
1961. Lodgepole pine in Alberta. Can. Dep. For. Bull. 127, 153 p.

Sorensen, F. C., and R. S. Miles.
1974. Differential frost tolerance of ponderosa and lodgepole pine megasporangiate strobili. For. Sci. 20:377-378.

Stark, R. W.
1954. Distribution and life history of the lodgepole needle miner (*Recurvaria* sp.) *(Lepidoptera: Gelechiidae)* in Canadian Rocky Mountain parks. Can. Entomol. 86:1-12.

Stark, R. W., and D. L. Wood.
1964. The biology of *Pissodes terminalis* Hopping *(Coleoptera: Curculionidae)* in California. Can. Entomol. 96:1,208-1,218.

Stelck, C. R.
1967. The record of the rocks. *In* Alberta, a natural history. p. 21-51. The Patrons, Edmonton.

Stephan, B. R.
1976. Zur intraspezifischen Variation von *Pinus contorta* auf Versuchsflächen in der Bundesrepublik Deutschland I. Ergebnisse aus der Versuchsserie von 1960/61. Silvae Genet. 25:201-209.

Stephens, F. R.
1966. Lodgepole pine-soil relations in the northwest Oregon Cascade Mountains. J. For. 63:184-186.

Stock, M. W., J. D. Guenther, and G. B. Pitman.
1978. Implications of genetic differences between mountain pine beetle populations to integrated pest management. *In* Theory and practice of mountain pine beetle management in lodgepole pine forests, p. 197-201. For., Wildl., and Range Exp. Stn., Univ. Idaho, Moscow.

Street, H. E., and J. Webb.
1975. Applications of plant tissue culture in forestry. *In* For. Comm. Rep. on For. Res., 1975, p. 58-59 (Great Britain).

Street, H. E., and J. Webb.
1976. Applications of plant tissue culture in forestry. *In* For. Comm. Rep. on For. Res., 1976, p. 58-59 (Great Britain).

Street, H. E., and J. Webb.
1977. Applications of plant tissue culture in forestry. *In* For. Comm. Rep. on For. Res., 1977, p. 53-54 (Great Britain).

Sweet, G. B., and P.F. Wareing.
1968. A comparison of the rates of growth and photosynthesis in first-year seedlings of four provenances of *Pinus contorta* Dougl. Ann. Bot. 32:735-751.

Sziklai, O.
1976. Forest genetics and tree breeding at the Faculty of Forestry, University of British Columbia. *In* Proc. 15th Meet. Can. Tree Improv. Assoc. part 1, p. 187-188.

Tackle, D.
1954. Viability of lodgepole pine seed after natural storage in slash. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Res. Note 8, 3 p. Ogden, Utah.

Teich, A. H.
1970. Cone serotiny and inbreeding in natural populations of *Pinus banksiana* and *Pinus contorta*. Can. J. Bot. 48:1,805-1,809.

Teoh, S. B., and H. Rees.
1976. Nuclear DNA amounts in populations of *Picea* and *Pinus* species. Heredity 36:123-137.

Terasmae, J.
1973. Notes on late Wisconsin and early Holocene history of vegetation in Canada. Arct. and Alp. Res. 5:201-222.

Thompson, S.
1976. The results of recent studies into the shoot elongation and dry matter production of two contrasted provenances of lodgepole pine. *In Pinus contorta* provenance studies, p. 43-51. For. Comm. Res. and Dev. Pap. 114 (Great Britain).

Thorne, R. F.
1977. Montane and subalpine forests of the Transverse and Peninsular ranges. *In* Terrestrial vegetation of California. p. 537-577. M. G. Barbour and J. Major, eds. John Wiley and Sons, New York and London.

Tigerstedt, A. F.
1922. [Arboretum Mustila. Report on experiments with trees and shrubs of foreign origin 1901-1921 I. Conifers.] Acta For. Fenn. 24, 231 p. [In Fin., Engl. summ.].

Tigerstedt, C. G.
1927. *Pinus murrayana*. Forstl. Tidskr. 44:31-48.

Trappe, J. M., and R. W. Harris.
1958. Lodgepole pine in the Blue Mountains of northeastern Oregon. U.S. Dep. Agric., For. Serv. Pac. Northwest For. and Range Exp. Stn., Res. Pap. 30, 22 p. Portland, Oreg.

Tree Breeding Committee [Finland].
1976. Proposed tree breeding programme in Finland, 1976-1985. Folia For. 266, 24 p., Helsinki.

Tzschacksch, O., M. Vogl, and K. Thümmler.
1969. Vorselektion geeigneter Provenienzen von *Pinus contorta* Douglas (*Pinus murrayana* Balf.) für den Anbau in den Rauchschadgebieten des oberen Erzgebirges. Arch. Forstwes. 18:979-982.

Uyeki, H.
1927. The seeds of the genus *Pinus*, as an aid to the identification of species. Bull. Agric. and For. Coll., Suigen, Corea, No. 2, 129 p.

Vester, G., and R. M. M. Crawford.
1978. Verschiedene Proveniezen von *Pinus contorta* Loudon und Überflutungsstress: Klassifikation auf Grund morphologischer und metabolischer Kriterien. Flora 167:433-444.

Viereck, L. A., and E. L. Little, Jr.
1972. Alaska trees and shrubs. U.S. Dep. Agric., For. Serv., Agric. Handb. 410, 265 p.

Von Rudloff, E.
1975. Volatile leaf oil analysis in chemosystematic studies of North American conifers. Biochem. Syst. Ecol. 2:131-167.

Von Rudloff, E., and E. Nyland.
1979. Chemosystematic studies in the genus *Pinus*. III. The leaf oil terpene composition of lodgepole pine from the Yukon Territory. Can. J. Bot. 57:1,367-1,370.

Von Weissenberg, K.
1972. Experiences of lodgepole pine in Finland. Meet. Nordic Work. Group Prov. Res. and Seed Procur. 73 p. Suonenjoki, Finland. [Varparanta, Finland, Aug. 15-19, 1972].

Waddington, J. C. B., and H. E. Wright, Jr.
1974. Late Quaternary vegetational changes on the east side of Yellowstone Park, Wyoming. Quat. Res. 4:175-184.

Wass, E. F.
1976. Ecology of shore pine stands infested with dwarf mistletoe on southeastern Vancouver Island. Can. For. Serv., Pac. For. Res. Cent., BC-X-142, 33 p. Victoria.

Wells, S. D., and J. D. Rue.
1927. The suitability of American woods for paper pulp. U.S. Dep. Agric., Dep. Bull. 1185, 102 p.

Westman, W. E., and R. H. Whittaker.
1975. The pygmy forest region of northern California: studies on biomass and primary productivity. J. Ecol. 63:493-520.

Wheeler, N. C.
1979. The lodgepole pine improvement program in British Columbia. 17th Meet. Can. Tree Improv. Assoc., Members' Rep., 5 p.

Wood, R. F.
1955. Studies of North-west American forests in relation to silviculture in Great Britain. For. Comm. Bull. 25, 42 p. (Great Britain).

Wood, S. L.
1963. A revision of the bark beetle genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). Great Basin Nat. 23:1-117.

Wright, H. E., Jr.
1964. Aspects of the early postglacial forest succession in the Great Lakes region. Ecology 45:439-448.

Wright, J. W., and W. J. Gabriel.
1958. Species hybridization in the hard pines, series *Sylvestres.* Silvae Genet. 7:109-115.

Yeatman, C. W.
1967. Biogeography of jack pine. Can. J. Bot. 45:2,201-2,211.

Yeatman, C. W., and M. J. Holst.
1972. Hardiness of jack pine hybrids and provenances in the boreal forest. For. Chron. 48:30-31.

Yim, K. B.
1961. Air-layering of lodgepole pine and origin of adventitious roots. For. Sci. 7:227-231.

Zavarin, E., W. B. Critchfield, and K. Snajberk.
1969. Turpentine composition of *Pinus contorta* × *Pinus banksiana* hybrids and hybrid derivatives. Can. J. Bot. 47:1,443-1,453.

*U.S. GOVERNMENT PRINTING OFFICE: 1980-0-325-980/6916

Reference Abstract

Critchfield, William B.
1980. Genetics of lodgepole pine, USDA For. Serv. Res. Pap. WO-37, 57 p.

The genetics and reproductive biology of lodgepole pine are reviewed, with emphasis on: wide distribution and occurrence in ecologically extreme habitats, relatively small size and short life, great dispersal ability, opportunistic role after deglaciation or forest fires, differentiation into several distinct but interfertile races, influence of introgression from jack pine, and suitability of some races for use in short-rotation plantations. Improvement programs in North America are just beginning; in northwestern Europe and elsewhere the primary objective of improvement is the choice of suitable provenances.

KEYWORDS: *Pinus contorta*, geographic variation, provenance tests, improvement programs.

NATIONAL AGRICULTURAL LIBRARY
1022895278

NATIONAL FOREST SYSTEM COOPERATIVE FORESTRY FORESTRY RESEARCH
FOREST SERVICE
U S
DEPARTMENT OF AGRICULTURE